THE DIVERSITY AND PHYLOGENY OF THE PATERINATE BRACHIOPODS

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ABSTRACT. The chemico-structure and morphology of the shells of the earliest known brachiopods, the paterinates, have many features consistent with the antiquity of the group and its phylogenetic proximity to the ancestral stock of the phylum. The organophosphatic shell is typically finely laminated and imprinted throughout with outwardly convex epithelial casts in the older cryptotretids. The greatest concentration of amino acids occurs in the shells of Ordovician *Dictyonites* but the higher level of aspartic acid/asparagine may not be related exclusively to the post-Cambrian age of the genus as the shell is uniquely 'perforate' through periodic reductions in phosphatic secretion. The quadrilobate larval dorsal valve, the interareas with delthyria and notothyria variably covered by homeodeltidia (or pseudodeltidia in some cryptotretids) and rarer homeochilidia suggest rhynchonelliform affinities as do mantle canal impressions and a musculature which included diductors implanted dorsally on the median plate within the notothyrium. Phylogenetic analysis with penecontemporaneous linguliforms and rhynchonelliforms as outgroups indicates that the paterinates are a sister group of the lingulates and consist of two subclades, Paterinidae and Cryptotretidae. The latter were short lived but remarkably diverse and may well have evolved directly from the brachiopod stem group.

PATERINATE brachiopods have been of abiding interest to students of the phylum since they were first separated taxonomically from the kutorginids (Beecher 1891, p. 345). The group had already been recognized as among the oldest metazoans to be represented by biomineralized remains in the geological record. Beecher (p. 346), however, regarded the semi-elliptical shell of *Paterina*, allegedly with all growth lines 'unvaryingly parallel and concentric, terminating abruptly at the hingeline' (hemiperipheral) as preserving throughout ontogeny the essential features of the embryonic shell (protegulum) and, therefore, as fulfilling a prototypic role in brachiopod phylogeny. *Paterina* was further characterized as having the simplest type of pedicle opening (Beecher p. 352); it effectively typified Beecher's new group, the Atremata.

Beecher's views on paterinate morphology were soon refuted. Walcott (1912, p. 339), found that the pedicle opening was restricted by a pseudointerarea (henceforth referred to as 'interarea', see section on '*Posterior margins*'); while Thomson (1927, p. 50), after concluding that growth of the ventral valve changed from hemiperipheral to holoperipheral during ontogeny, transferred the paterinids from the Atremata to the Neotremata. Yet the most intriguing aspect of the group, its mixture of features generally accepted as mutually exclusive to either inarticulated or articulated brachiopods, was not explicitly discussed until Bell (1941, p. 213) erected a genus, *Icodonta*, on the presence of sockets in the dorsal valve of the type species. This was refuted by Rowell (1965, p. H295), although he drew attention to the posteriomedial grouping of the muscle scars in the manner of articulated brachiopods and figured two versions of possible soft tissue relationships within the posterior part of the shell (p. H90).

Rowell (1980) has since elaborated this theme with the aid of well preserved *Dictyonina pannula* (White) from Nevada. He noted that, apart from their organo-phosphatic shells, paterinates are essentially articulated brachiopods in the taxonomic sense. In particular, he emphasized the strophic relationships of the interareas but, in the absence of unambiguous diductor scars from both valves, believed that the shell may not have opened orthodoxly. Rowell (p. 18) was also the first to identify ventral *vascula media*. Their presence was confirmed by Laurie (1987) who figured beautifully

preserved Australian paterinates revealing their orthide-like mantle canal systems and muscle scars. He contended that the variable disposition of the interareas among paterinates generally was consistent with an orthodox lever action for the opening of the valves.

The advances made through the studies of American and Australian paterinids were simultaneously being complemented by the researches of Russian palaeontologists.

The earliest brachiopods yet recorded are *Aldanotreta* and *Cryptotreta* (Pelman 1977) from the Tommotian Stage of north-central Siberia. Only *Aldanotreta* was confidently identified as a paterinid but Pelman later (1979) erected Cryptotretidae to include both genera and assigned the family to the Paterinida. The first ultrastructural studies of the shell (Popov *et al.* 1982) revealed the distinctive tuberculate ornamentation of paterinid larval shells. Popov and Ushatinskaya (1987) published a preliminary report on the paterinate skeletal fabric although all shells at their disposal had been recrystallized except for that of *Cryptotreta* which appeared to be composed of stratiform laminae of close-packed prisms.

These historical uncertainties and contradictions about paterinate affinity greatly handicap attempts to establish a phylogenetic classification of the Brachiopoda (Williams *et al.* 1996). The main contradiction is the organophosphatic composition of a shell that is strophic yet also bears the imprints of a muscle system like that of early Palaeozoic articulated species. In the wider context, the composition and morphology of Early Palaeozoic shells are currently being investigated by all four authors of this paper. It therefore seemed opportune to collaborate in a comprehensive review of the composition and functional morphology of the paterinate shell in expectation that some of the past uncertainties would be resolved.

We have concluded that: the paterinid shell consisted of stratiform laminae, probably with a higher organic content than that of living organophosphatic species; the valves articulated on a periostracal axis along a strophic hinge line; the paterinid larva was probably closer to that of rhynchonelliforms than linguliforms. The phylogenetic relationships among paterinids, crypto-tretids and contemporaneous calcitic-shelled brachiopods are still in some doubt.

MATERIALS AND METHODS

Paterinates are ubiquitously represented in Cambrian successions by at least seven genera, four of which, classified as cryptotretids, are restricted to the Lower Cambrian and include the first recorded brachiopods within the fossil record. Three genera also occur in the Ordovician with *Kolihium* and *Lacunites* restricted to the Tremadoc and only *Dictyonites* ranging throughout the system. Although widely distributed, these brachiopods which were rarely more than a few millimetres long, were never dominant members of fossil assemblages. Their phosphatic shells, however, can be dissolved out of carbonate rocks; and the great majority of specimens investigated by us were recovered from residues etched in an aqueous solution of acetic acid (10 per cent. by volume).

Materials

Specimens (including type material) of all genera, except *Dzunarzina* Ushatinskaya, possibly synonymous with *Askepasma* and *Kolihium* Havlíček, were studied for the preparation of the section on paterinate morphology. However, only small quantities of broken shells were available for chemico-structural investigations and their identification and provenance are listed below. Taxa that have been studied and frequently figured ultrastructurally are prefixed by a single asterisk; those additionally analysed biochemically, by a double asterisk.

Aldanotreta sunnaginensis Pelman; Lower Cambrian, Tommotian, Pestrotsvetnaaja Formation, south side of Aldan River, Dvortsy, Siberia.
Aldanotreta sp.; Lower Cambrian, Ajax Limestone, Flinders ranges, Australia.
Aldanotreta? *phillipsii* (Holl); Lower Cambrian, Comley Series (Hollybush Sandstone), England.

**Askepasma toddense* Laurie; Lower Cambrian, Todd River Dolomite, Deep Well, Northern Territory, Australia.

Cryptotreta undosa (Moberg); Lower Cambrian, Upper Tommotian–Lower Atdabanian, Kalmarsund Sandstone, Kalmarsund, Sweden.

Cryptotreta sp.; Lower Cambrian, Atdabanian, Tjuser Formation (sample NL-2/6), Neleger rivulet, east side of Lena River, north-central Siberia.

Dictyonina hexagona (Bell); Middle Cambrian, Amgian, *Ptychagnostus intermedius* Zone (sample 1465), Kyrshabakty river, Malyi Karatau Range, Kazakhstan.

Dictyonina pannula (White); Middle Cambrian, Burgess Shale, British Columbia.

Dictyonina sp.; Upper Cambrian, Kety Regional Stage (Sample 5058), Botorchuk River, south of the village of Sukhona, north-central Siberia.

**Dictyonina*? sp.; Middle Cambrian, Unit 10, Frenchman Mountain (Longwell 1–59), Nevada.

Dictyonites fredriki Holmer; middle Ordovician, Furudal Limestone, Dalarna, Sweden.

***Dictyonites perforata* Cooper; middle Ordovician, Pratt Ferry Formation, Pratt Ferry, Alabama.

**Dictyonites* cf. *perforata* Cooper; middle Ordovician, Lower Llanvirn, Kurchilik Formation (Sample 145/3), Sary-Kumy, Kazakhstan.

Discinisca tenuis Jackson; Recent, washed up clusters of dead shell, Swakopmund, Namibia.

Lacunites balashovae Gorjansky; lower Ordovician, Billingen Stage, *Oepikodus evae* Zone (Sample 6817/7a), west side of Lava River near village of Vassilkovo, Ingria, north-west Russia.

Lacunites alimbeticus (Andreeva); lower Ordovician, Arenig, Kuragan Formation (sample 800–4), eastern side of Karakol River near the village of Baitas, South Urals.

**Micromitra* sp.; Middle Cambrian, (*Paradoxides forchammeri* Zone), Råbäck, Västergötland.

Micromitra cf. *modesta* (Lochman); Upper Cambrian, *Elvinia* Zone (locality no. 872), Nevada.

**Micromitra* cf. *ornatella* (Linnarsson); Middle Cambrian, Sosiuk Formation, Turkey.

***Micromitra pusilla* (Linnarsson); Middle Cambrian, Andrarum Limestone, Olea, Bornholm, Denmark and Andrarum, Scania, Sweden.

***Micromitra*? *semicircularis* Imanaliev and Pelman; Lower Cambrian, Toyonian, Middle Cambrian, Mayaian, Zhalgyz Formation (Locality 5875), Suuk-Adyr Mountains, Kazakhstan,

***Micromitra* sp.; Middle Cambrian, Arthur Creek Formation, south-west Georgina Basin (sample H583), Australia.

Micromitra sp.; Middle Cambrian, *Bathyuriscus-Elrathina* Zone, olistolith in the basal Los Sombreros Formation (sample LS 28), Salta District, Argentina.

Paterina alaica Imanaliev and Pelman; Middle Cambrian, Karagaily Formation (sample 1639), Kastek Range, North Tien-Shan, Kirgizia.

Paterina labradorica (Billings); Lower Cambrian (locality no. 41k), Labrador.

Paterina sp.; Lower Cambrian, Comley Series, England.

Paterina sp.; Middle Cambrian, Grove Crick Limestone (locality no. G4), Beartooth Butte, Toll, Upper Park, USA.

**Paterina*? sp.; Lower Cambrian, Wilkawillina Limestone (Sample 19), Wilkawillina Gorge, Flinders Range, Australia.

Paterinid; Middle Cambrian, Knivinge Quarry, Östergötland, Sweden.

Salanygolina obliqua Ushatinskaya; Lower Cambrian, Botomian, Khairkhan and Salanygol formations, Salany-Gol rivulet, Khasagt-Khajran Rainge, Mongolia.

Terebratulide; Recent, intertidal sands, Connemara, Ireland.

Illustrated and discussed material is deposited in the following: Central Scientific Research Geologic Exploration Museum, St Petersburg (collection numbers CNIGR); Commonwealth Palaeobiological Collections, Canberra (CPC); Department of Stratigraphy and Historical Geology, National University Cordoba, Argentina (CEGH-UNC); Institute of Geological Sciences, Almaty, Kazakhstan (IGSA); Institute of Geology and Geophysics, Novosibirsk (IGIG); Palaeontological Museum, University of Uppsala (PM); Sedgwick Museum, Cambridge (SM); South Australian Museum, Adelaide (collection numbers SAM); Swedish Museum of Natural History, Stockholm (RMB); United States National Museum, Washington (USNM).

Residues of specimens used for chemico-structural investigations (including fragments mounted on stubs) are deposited in the Hunterian Museum, The University of Glasgow. The appropriate numbers are prefixed by GLAHM.

Methods

Chemico-structural investigations. The procedures adopted for preparing paterinate shells for ultrastructural studies under the SEM, energy dispersive spectrometer (EDS) analysis, and amino acid analysis, are those previously followed (Cusack and Williams 1996, p. 36). X-ray diffraction (XRD) determinations were carried out using a Philips PW 1050/35 XRD with a Co energy source (kα1·7902Å), Fe filter, vertical coniometer scanning 4°2θ to 60°2θ with a step of 0·02°2θ. Shells were powdered in acetone and the slurry poured on to a glass slide. For samples of low abundance, the shell powders were mixed with liquid paraffin and taken up into a glass capillary which was then inserted into a Debye Scherer camera and the film exposed to X-rays for 4 hours.

In previous chemico-structural studies involving shells of living species, stringent protocols have been followed to forestall and monitor microbial contamination (Williams *et al.* 1994, p. 263). During these analyses it became evident that the same procedures would also have to be adopted for fossil samples dissolved out of rock. In particular, we advocate that etched residues, immediately after washing and draining, should be dried in a laminar flow chamber.

Phylogenetic analysis. Ten paterinate genera, defined by 39 unweighted characters, each between two and five states in variability, have been analysed by the PAUP 3.1.1 program (Swofford and Begle 1993), supplemented by the MacClade 3.0 program (Maddison and Maddison 1992). Heuristic search options were undertaken with character transformations following ACCTRAN optimization. All characters were unordered during analysis, enabling polarity to be determined exclusively by outgroup methods (Appendix 1).

The choice of outgroups was determined by stratigraphical as well as palaeobiological considerations (Appendix 2). The paterinates include the geologically oldest brachiopods yet recorded, the Tommotian cryptotretids. However, other linguliform and rhynchonelliform groups are represented in slightly younger Cambrian successions and could have included the sister group of the paterinates.

Palaeobiologically, the choice of outgroups had to take into account the contradictions of the paterinate shell, its organophosphatic composition and its strophic hinge axis, which are mutually exclusive synapomorphies of lingulate and rhynchonelliform brachiopods. We have chosen the Early to Mid Cambrian genera, *Eoobolus*, *Fossuliella* and *Botsfordia* and the Mid Cambrian to early Ordovician *Obolus* to represent the full diversity of contemporaneous organophosphatic lingulates. The earliest recorded rhynchonelliforms, all characterized by strophic hinge axes and organocalcitic shells, are the Atdabanian chileates, obolellates and kutorginates.

EXPLANATION OF PLATE 1

Fig. 1. *Paterina*? sp.; GLAHM 101949; Lower Cambrian; Flinders Range, Australia; fracture section of a shell fragment showing the cleaved primary layer (pl) overlying a secondary layer (sl) of stratified and rubbly laminae; × 800.

Figs 2–3. *Micromitra* sp.; Middle Cambrian (Arthur Creek Formation); Australia. 2, GLAHM 101950; external view of recrystallized primary layer showing the spherular nature of mosaics (mc); × 26500. 3, GLAHM 101951; surface view of lithified periostracum and primary layer folded into periclinal folds (fd); × 1900.

Fig. 4. *Dictyonina*? sp.; GLAHM 101952; Middle Cambrian; Frenchman Mountain, Nevada; surface detail of a lithified, finely folded periostracum; × 25500.

Fig. 5. *Cryptotreta undosa* (Linnarsson); GLAHM 101963; Lower Cambrian (Kalmarsund Sandstone); Sweden; external view of mature dorsal valve showing fila (fm) and folds (fd) of the lithified periostracum and primary layer interrupted by nick points (nk); × 70.

Figs 6–8. *Micromitra* cf. *ornatella* (Linnarsson); GLAHM 101953; Middle Cambrian (Sosiuk Formation); Turkey; details of ornamentation on a mature dorsal valve with: 6, continuous fila (fm) raised along a radial costa (rb), immediately beyond the margin of the larval valve, × 250; and (7–8) two views, × 420, × 850, of depressions (dn) with pitted and folded back walls (bl).

PLATE 1
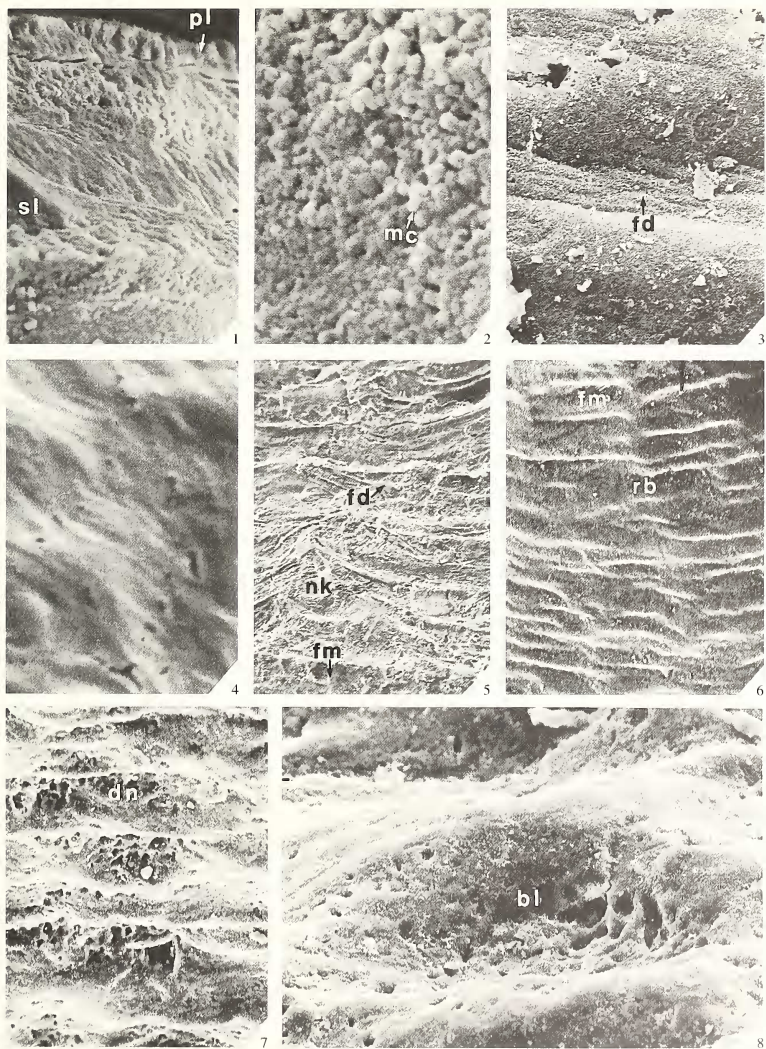
CHEMICO-STRUCTURE OF SHELL

The paterinates are thin-shelled brachiopods but not disproportionately so relative to their size when compared with other organophosphatic-shelled species. The thickness of the posteriomedial parts of mature valves of *Micromitra* or *Paterina* seldom exceeds 250 μm while peripheral to the body platform the shell is normally between 20 and 40 μm thick reducing to less than 10 μm beneath deeply indented ornament in *Dictyonina* or even to perforations in *Dictyonites*. Despite extensive recrystallization, enough of the original microfabric is preserved, or pseudomorphously replaced to indicate that the paterinate shell was secreted by the mantle and its outer marginal lobes in an orthodox succession of periostracum, primary, and secondary layers. This assumption underlies the following report on the chemico-structure of the paterinate shell. However, the secondary layer of the cryptotretids differs from that of the paterinids and is discussed separately.

Structure and inferred periostracum. During brachiopod shell secretion, the periostracum serves as a substrate for the succeeding primary layer. The oldest periostracum so far recorded is that of the Late Cretaceous *Sellithyris* (Gaspard 1982); but occasionally it can be inferred from superficial microstructures even of Palaeozoic organophosphatic shells, in which the primary layer acted rheologically and formed nanometric casts of its interface with the periostracum. In this context, some of the superficial microstructures of paterinate shells have been interpreted as casts of periostracal features and are best explained after the primary layer has been described.

Primary layer and ornamentation. The primary layer of the paterinate shell is not always clearly distinguishable as it may grade into the secondary layer without any sharp break. It is, however, usually identifiable as a homogeneous, compact, vertically cleaved 'patina' (Pl. 1, fig. 1) and averaged 5 μm in thickness (range 2·5–10·5 μm) in five paterinid genera and 1·8 μm in *Cryptotreta*. The basic biomineral components are spherular aggregates of granular apatite, normally 40–60 nm in diameter, which are variably aggregated into mosaics, more than 200 nm in diameter, or recrystallized into plates, a micrometre or so in size (Pl. 1, fig. 2).

Well-preserved surfaces of the primary layer are contoured not only by ornamentation but also by impersistent swarms of periclines up to 10 μm long and normally less than one micrometre in wavelength (Pl. 1, fig. 3). Even finer patterns of anastomosing ridges, 50 to 100 nm in wavelength, are preserved, albeit rarely (Pl. 1, fig. 4). Concentrically disposed swarms of periclines are generated by changes in the rate of periostracal secretion in living *Lingula*; and it is assumed that sets of the finer ridges are variations in the thickness of the basal layer of the periostracum. The replication of such features indicates that the paterinate primary layer had a fine enough consistency and plasticity to form faithful casts of features on a nanometric scale. This is also true of the primary layer of *Lingula* (Williams *et al.* 1994, p. 241), which consists of glycosaminoglycans (GAGs) and scattered spherular apatite. This then is likely to have been the original composition of the paterinate primary layer prior to phosphatization.

The basic microtopography of the paterinid primary layer consists of concentric asymmetrical fila with steep outer faces wrinkled by periclinal folds, 50 or more μm long, parallel with the filar crests. In *Micromitra*, for example, filar crests are 10–20 μm apart with approximately six periclines on the outer faces. The fila are usually broken by nick points into drapes (Williams and Holmer 1992) which also deform the fila and shell surface of cryptotretids (Pl. 1, fig. 5). Other paterinids are characterized by more fundamental changes in the basic pattern, especially the development of regularly occurring depressions (Text-fig. 1).

In *Micromitra* cf. *ornatella* about four unbroken, asymmetrical fila surround the larval shell. The steeper outer face of each filum may be finely striated more-or-less parallel with the long axis; the gently inclined inner surface may be up to 20 μm long radially. Narrow, radiating folds (ribs), initially about 70 μm apart, increasingly interfere with the fila (Pl. 1, fig. 6) which progressively break up into alternate, inner and outer arcs between 70 and 200 μm long. The arcs become concavely curved outwardly and are usually composed of several tight, concentric folds,
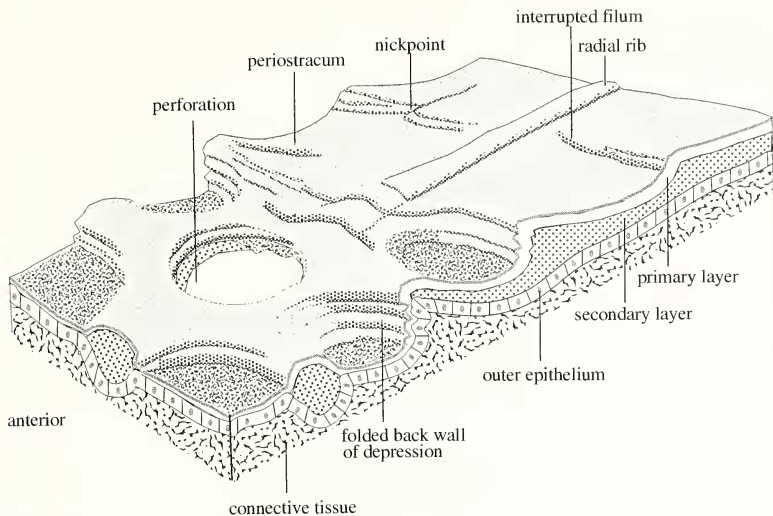
TEXT-FIG. 1. Diagrammatic representation of the inferred development of the ornamentation affecting the primary layer of the shells of the paterinids, *Dictyonina*, *Micromitra* and *Dictyonites*.

cumulatively up to 40 μm or so deep. They form back walls to gently inclined floors (Pl. 1, figs 7–8). Both floors and walls are variably indented and together delineate depressions varying in size and outline from broadly elliptical, about 30 μm and 40 μm in axial dimensions, to lanceolate with major axes up to approx. *c*. 120 μm. These depressions occur quite regularly in alternating concentric rows with anastomosing, tightly folded boundaries.

The microtopography of another species, *Micromitra pusilla*, is like that of *M*. cf. *ornatella* with elliptical depressions (axes averaging 60 μm and 40 μm) occurring in concentrically alternating sets and delineated by tightly folded back walls and variably inclined floors (Pl. 2, figs 1–3). The floors of the depressions, however, are not as deeply indented while the shell surface is further folded along two axial sets subtending an angle of about 120° and disposed orthogonally to the lateral margins,with wavelengths of about 20 μm and with crests at intervals of about 70 μm.

The shell of *Dictyonites* (Pl. 12, figs 11–13) is ornamentally distinguishable from those of other paterinids by being perforated (Pl. 2, figs 4–5). The sub-circular perforations are large, averaging about 75 μm and 175 μm respectively in the mid-shell regions of Siberian and American species, and are arranged in offset radiating rows (Wright 1981, p. 445). Within this regular pattern, deep depressions occur instead of some perforations and are a clue to the development of this unique ornamentation (Pl. 2, fig. 6).

The depressions are not hemispherical but asymmetrical 'basins' with steep back walls and floors gently inclined towards the shell margin. The back walls are transversely folded into periclines, up to 6 μm in wavelength, which also wrinkle the surfaces of the intervening walls (Pl. 2, fig. 6). The external surfaces of these depressions are microscopically smooth with compacted granular apatite variably recrystallized into flat-lying plates. An internal view of the depressions shows them as relatively smooth 'domes', bearing the casts of the periclines of the back walls, which contrast with

the low-lying roughened internal surfaces of their bounding walls (Pl. 2, fig. 7). The shell forming the 'domes' is seldom more than 3 μm thick and consists of granular apatite and clay grading into a recrystallized zone of plates and prisms at the 'dome' surfaces (Pl. 3, fig. 3) in contrast to the clays and mosaics of pinacoids on the inner surfaces of the bounding walls (Pl. 3, fig. 4).

The surface of the rim of a typical perforation normally bears a ragged break between a finely folded outer band and a granular inner one (Pl. 3, figs 1–2). This suggests that, in life, the perforations were sealed by a thin, mainly organic layer, now lithified (Pl. 3, fig. 1) which would have formed the external coat of depressions in the imperforate parts of the shell. The surfaces of some rims, however, bear casts of growth banding and periclines, which appear to be unbroken (Pl. 3, fig. 5). Presumably the protective covers of the patches of outer epithelium underlying such perforations would have been membranous and attached to the rims of perforations at their junctions with the valve interior.

The superficial microstructure of the *Askepasma* shell is different from that of *Dictyonina* and *Micromitra*. It consists of hexagonally close-packed, hemispherical hollows (Pl. 3, figs 6–7), *c.* 7 μm in diameter and *c.* 3 μm deep, separated from one another by a network of rounded walls *c.* 2 μm thick and composed of compacted apatitic spherules and recrystallized pinacoids (Pl. 4, fig. 3). Eight to thirteen domed bodies, about 1 μm in size and sporadically studded with apatitic spherules, are frequently found on the floors of the hollows (Pl. 4, figs 1–2). A striated layer forming gently convex covers over the hemispherical hollows is rarely preserved (Pl. 3, fig. 7). The network evidently acted in life as an integral, plastic sheet. Thus, its hexagonal pattern was distorted by changes in the slope of the shell and it has even been lifted and ruptured by recrystallized protrusions of the primary layer. The sheet also appears to have been stretched over fila where its network may become smoothly taut (Pl. 3, fig. 6).

The depressions on the shell surfaces of *Dictyonina*, *Micromitra* and *Dictyonites* are homologous (Text-fig. 1). They form offset radiating arrays indenting the outer, periclinally folded faces of concentric fila and originated in the angles subtended by two sets of obtusely disposed microscopic ripples affecting the mantle margins.

Microstructural evidence suggests that the depressions indenting the paterinid shell were occupied by bodies with sufficient weight or turgidity to flatten periclinal fold systems. Such bodies, however, would have ranged from 50 μm to more than 200 μm in size; and no known secretory system in living species is capable of incorporating comparable structures within a periostracum. Even setae in their follicles, at about 25 μm in diameter, are too small to have played the rôle of bodies transiently attached to the periostracum at the mantle edge should that have been topologically possible. We have, therefore, concluded that these depressions signify nothing more than periodic sags of a crenulated mantle margin along radial vectors offset by cross ripples. Their development is assumed to have been similar to the hollow ribs (aditicules of Wright 1981) in some orthide groups as interpreted by Williams and Rowell (1965). Accordingly, the periostracal base which served as substrate for the primary layer of such paterinates, would have lacked any infrastructure and would have carried no evidence of a superstructure. Indeed the thin layer, forming the 'domes' of

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EXPLANATION OF PLATE 2

Figs 1–3. *Micromitra* sp.; GLAHM 101955; Middle Cambrian (*P. forchammeri* Zone); Sweden. 1, general view of ornamentation on a shell fragment; × 65. 2–3, details of arcs of depressions (dn) with folded back walls (bl) raised along costae (rb); × 220, × 1000.

Figs 4–7. *Dictyonites perforata* Cooper; middle Ordovician (Pratt Ferry Formation); Alabama. 4–5, GLAHM 101956; views of internal surfaces of fragments of a mature dorsal valve showing perforations (pn) with the secondary layer (sl) and remnants of lithified periostracum and primary layer (pl) exposed along edges of perforations; × 120, × 480. 6–7, GLAHM 101957; external and internal views of asymmetrical, basin-like depressions (dn) delineated by lithified periostracum and primary layer (pl) with folded backwalls (bl), structurally distinguishable from secondary layer (sl); × 110, × 160.

PLATE 2

WILLIAMS *et al., Micromitra, Dictyonites*
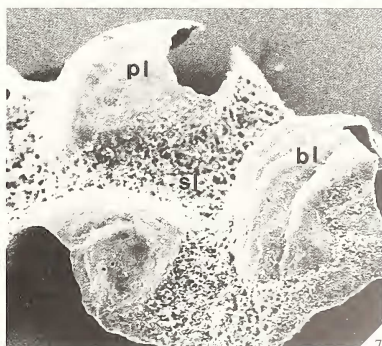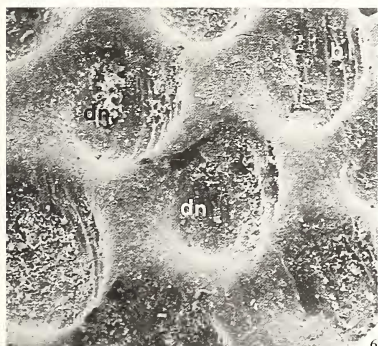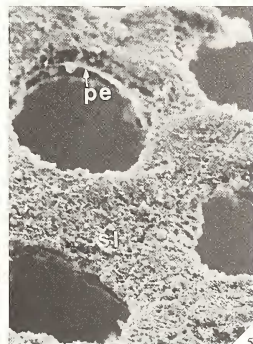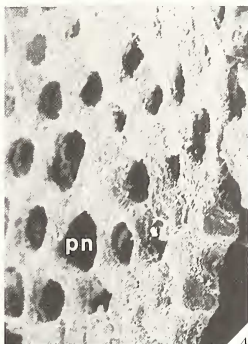
Dictyonites (and the membranes that presumably sealed the perforations), is probably a phosphatized relict of the periostracum and primary layer (Pl. 2, figs 6–7). The internal junction between the primary and secondary layers is well defined around the bases of the 'domes' (Pl. 2, fig. 7) and presumably coincides with the boundaries of patches of outer epithelium which did not secrete secondary shell but remained attached by hemidesmosomes to a largely organic primary layer.

The hexagonally packed hollows of *Askepasma* indent the entire external surface including the larval shell where they differ only in being less regular as a result of much wrinkling. The umbonal presence of these depressions is reminiscent of the hemispherical pits indenting acrotretoid larval shells. These pits are assumed to have been casts of periostracal vesicles exuded during the early stages of larval shell secretion (Biernat and Williams 1970). They vary from 250 nm to 5 μm in diameter but are never so uniformly distributed or so large as the hollows of *Askepasma*. Indeed, the shape and size of hollows are consistent with their having been moulded on the outer mantle lobe by vesicular cells that were more cuboidal than those found in living discinoids and linguloids. According to this interpretation, the hexagonal network of walls represents phosphatized deposits occupying the sites of intercellular spaces, and the floors of the hollows, with their scattered domes, the respective sites of apical plasmalemmas with erect extensions, rather like the more, finely tubular plasmalemmas of living species (Williams *et al.* 1992).

We conclude that the surface ornamentation of *Askepasma* is the cast of a complexly moulded basal layer of a periostracum and has been preserved by phosphatization of a thin primary layer. Both periostracum and primary layer would have been highly plastic in the living state as both appear to have been subjected to stretching and flow over fila. The rarely preserved striated covers to the hollows are tentatively homologized with pellicles secreted by inner epithelium in living brachiopods (Williams and MacKay 1979, p. 723). No such moulding affected the periostracal basal layer of paterinids (Pl. 1, fig. 4).

Secondary layer. The secondary layer of the cryptotretid shell has been described by Popov and Ushatinskaya (1987) and Ushatinskaya (1995) as a succession of laminae composed of close-packed hexagonal columns, 6–8 μm in diameter. The absence of columns from the secondary layers of other paterinates was attributed to their destruction by recrystallization. Study of the secondary layers of *Cryptotreta undosa* and *Cryptotreta* sp. compared with those of paterinids, however, suggests that the structures were not columnar and that their widespread absence among paterinids is due to the prevalence of other kinds of lamination.
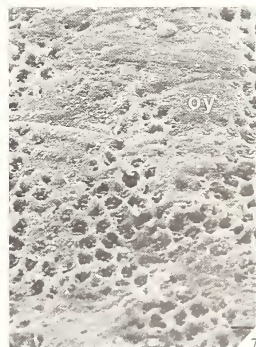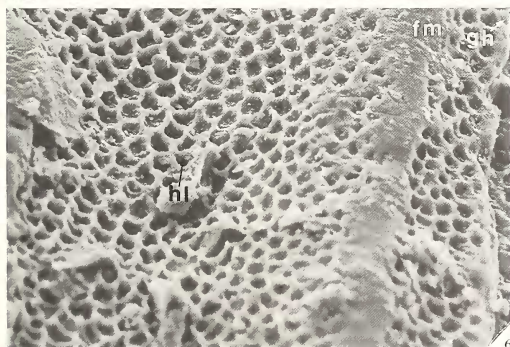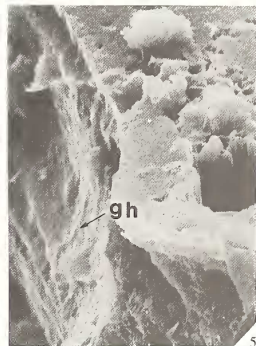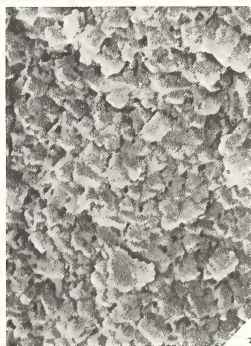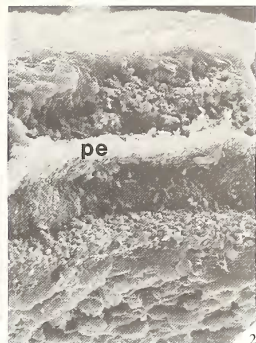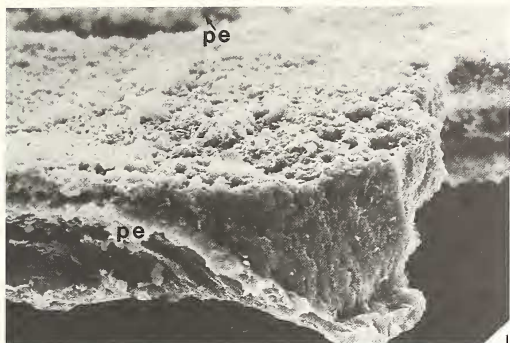
The secondary layer of *Cryptotreta* is essentially a finely stratified succession of horizontally disposed, phosphatized 'membranes', 80–100 nm thick, alternating with apatitic laminae up to 2 μm thick (Pl. 4, figs 4, 7).

The lithified membranes are almost invariably indented by low features 5–8 μm in diameter (Pl. 4, figs 4–5). The features vary in outline from hexagonal to circular or elliptical domes or depressions. Domes are typical of surfaces viewed from the exterior (Pl. 4, figs 4–5) and depressions

PLATE 3

WILLIAMS *et al.*, *Dictyonites, Askepasma*

of internal surfaces (Pl. 5, fig. 4). The domes, which are commonly asymmetrical with the steeper parts facing outwards, may overlap one another or amalgamate into convex sinuosities. These features occur throughout shell successions and on all exposed, sub-primary surfaces.

The apatitic laminae vary in thickness. They could originally have been little more than a monolayer of spherules, 100 nm or so in diameter (Pl. 4, figs 6–7) although they are now mostly recrystallized into acicular prisms of apatite, up to 700 nm long, disposed orthogonally to, or parallel with, the phosphatized membranes (Pl. 5, fig. 2). In the mid-parts of mature shells, apatitic laminae may pass into lenticular chambers, up to 25 μm high, with walls of orthogonally disposed acicular apatite enclosing aggregates of clays and apatitic prisms (Pl. 5, fig. 3). Successions may also be recrystallized into spherulites of acicular apatite, 2–3 μm in diameter, retaining only traces of the original lamination (Pl. 5, fig. 5).
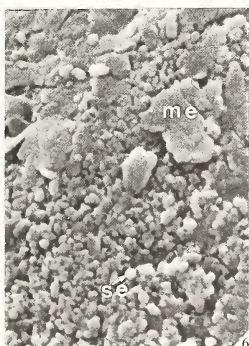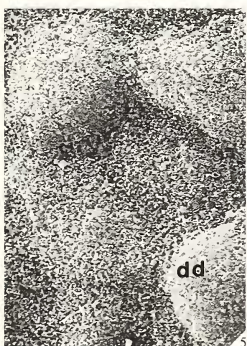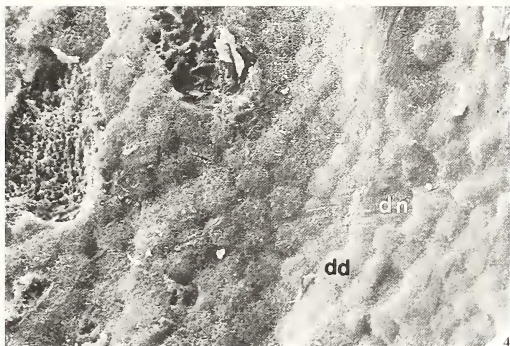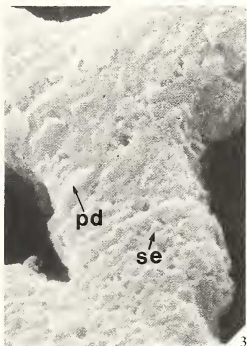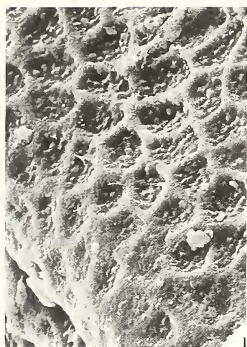
The features on the membranes were impressed by cells of mantle epithelium, typically rhombic or hexagonal in arrangement but deformed into domes and depressions by differential secretion of apatite onto successive membranous substrates. The overlap and sporadic amalgamation of asymmetrical domes indicate that the epithelium was mobile relative to the shell. This relationship is consistent with the absence of the canal system found in other linguliforms. Moreover, the acicular recrystallization of the cryptotretid shell suggests that the basic unit of apatite, *in vivo*, was associated with a more easily degradable organic matrix than in other linguliforms (possibly including even the paterinids).
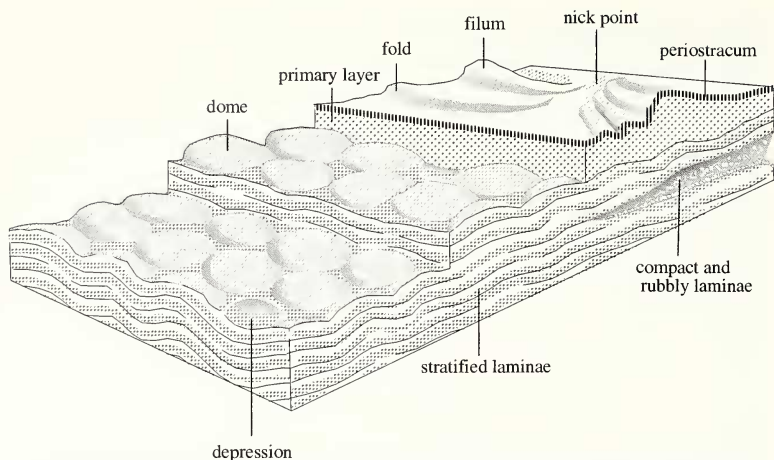
A succession of stratified laminae bearing casts of epithelial cells may simulate stacks of hexagonal columns. The effect can be exaggerated by the presence of sporadically distributed shallow pits along the crests of fila (Pl. 5, fig. 1). Such pits, however, are as likely to be either diagenetic solution hollows or original depressions initiated by low rates of secretion as in craniid shells (Williams and Wright 1970). Indeed, depressions are not unique to cryptotretids as they have been found in an Australian *Paterina*, (Pl. 5, figs 6–7). In this species, shallow hexagonal depressions, 5–10 μm in diameter are impressed on all exposed internal surfaces of a secondary layer, up to 250 μm thick, in the posteriomedial region of the shell occupied by paterinate muscle bases. The hexagonal imprints have the same disposition and dimensions as impressions underlying the adductor bases of *Neocrania* (Williams and Wright 1970, p. 26) and *Lacazella* (Williams 1973, p. 457) but are only half the size of the casts of mantle epithelium found in the anterior and lateral parts of the shells of living and fossil lingulids (Curry and Williams 1983, p. 112). Similar imprints have also been found in *Askepasma and Micromitra* (Pl. 6, fig. 2) but never with the same clarity or ubiquity as the impressions on cryptotretid secondary shell surfaces. Persistent hexagonal imprints found in paterinid shells are presumably the casts of epithelium associated with muscle bases.

The original apatitic constituents of the paterinid secondary layer of other paterinates have been determined by taking into account the general as well as the specific effects of recrystallization. Firstly, specimens of Swedish *Micromitra*, used in this investigation, were etched from the same rock samples as *Acrothele*, *Linnarssonella* and *Prototreta*, shells with microstructures indistinguishable

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PLATE 4

WILLIAMS *et al., Askepasma, Cryptotreta*

TEXT-FIG. 2. Diagrammatic representation of the inferred shell structure of cryptotretid paterinates.

from the basic skeletal components of Late Palaeozoic and living lingulates. As the shells of these contemporaneous and Recent species are also organophosphatic and of comparable thicknesses, we have assumed that the skeletal ultrastructure of paterinates, from the same assemblages as Cambrian acrotretoids and linguloids, would have also retained traces of the original microfabric.

Secondly, degradation of any of the intercrystalline organic matrix of these shells would have given rise to voids within the skeletal successions, which would have been filled by pseudomorphous mineral assemblages. Some of these are clays (Pl. 5, fig. 3) but the dominant replacements were variably developed apatitic plates with recognizable spherules of apatite in various stages of engulfment (Pl. 6, fig. 6).

The prime source of minerals, composing such plates and various crystallized bodies within or on the shells, is believed to have been apatitic granules and spherules, with a size range of 5–50 nm, originally disseminated throughout the organic matrix as in Recent species. Relicts of spherules are commonly found in plates, while clusters of hexagonal prisms and pinacoids, 50–200 nm in size (Pl. 6, fig. 3), are interpreted as crystallized pseudomorphs of spherules. In effect, even recrystallized shells often afford some guidance as to their original ultrastructure. Identification of the paterinate biomineral as carbonate hydroxylapatite indicates that any authigenic apatite is likely to have the same chemical composition as the original.

The fine structure of the posteriomedial successions (with hexagonal imprints) of the Australian *Paterina* consists of closely packed spheroidal apatite, 40–180 nm in diameter with minor patches of an apatitic matrix and clays (Pl. 5, fig. 8). The succession is poorly cleaved vertically and segregated into stratiform units, usually about 4 μm thick but ranging between 2 μm and 10 μm. The ultrastructure of the equally thick posteriomedial shells of the Australian *Askepasma* (Pl. 6, fig. 1) is similar.

In thinner, more marginal parts of shells, apatitic constituents tend to be more loosely aggregated and evidence of membranous lamination more obvious. Thus, within 20 μm of, and more or less parallel with, the internal margin of one valve of a Swedish *Micromitra*, a rounded ridge, up to 3 μm wide, was found (Pl. 6, fig. 2). The ridge is composed of spherular aggregates, partly incorporated

into pinacoidal plates or recrystallized as prisms. It separates an inner, more finely textured, platy sheet from a more open, outer layer with clays and voids as well as spherular aggregates (Pl. 6, fig. 3). The inner layer is texturally akin to the marginal surface which represents the primary layer.

We have interpreted the *Micromitra* sequence as follows. The inner layer was a membranous lamina, the edges of which curled into a ridge on the death of the animal and were phosphatized during fossilization. This lamina was secreted on a sub-primary lamina originally composed of apatitic mosaics and spherules in a GAGs matrix. Both laminae together constitute the basic cycle of secretion in the paterinid shell; while rhomboidal impressions on the inner lamina (Pl. 6, fig. 2) are outlines of infra-marginal, outer epithelial cells. The succession in an oblique marginal section of another valve of *Micromitra* supports this interpretation, as one lamina looks like a lithified wrinkled membrane (Pl. 6, fig. 4). In the Turkish *Micromitra*, spheroids more than 800 nm in diameter and composed of spherular aggregates less than one-tenth that size, can form clusters separated by voids in laminae 25 μm thick (Pl. 6, fig. 5). Successions in other paterinids also consist of subhorizontal apatitic plates with intervening layers of spheroids. The perforated shell of the American *Dictyonites* is usually more completely recrystallized than those of other paterinates (Pl. 6, fig. 6). However, a microfabric of fine lamination interleaved with apatitic spheroids and prisms and clays is discernible in successions less than 20 μm thick (Pl. 6, fig. 8). The thickened surrounds of the perforations are characterized by a distinctive rubbly fabric dominated by close packed spherules or recrystallized replacements (Pl. 6, fig. 7).

In summary, the shell structure of cryptotretids originally differed from that of paterinids in the occurrence of epithelial imprints on the surfaces of membranes throughout the secondary layer (Text-fig. 2). The successions also differ in the prevalence of stratified and compact to rubbly lamination in the cryptotretid and paterinid shells respectively although this distinction is less exclusive. The occurrence of imprints may be due to the continuing secretion of membranous constituents along intercellular pathways after the start of exocytosis of skeletal constituents through the apical plasmalemmas of the outer epithelium. Successions of such imprints are not unique, being characteristic, for example, of contemporaneous *Lingulella* (Curry and Williams 1983).

The mineral phase of *Dictyonites perforata* from the Pratt Ferry Formation, *Micromitra semicircularis* from Kazakhstan, *Askepasma toddense* from Australia, *Micromitra pusilla* from the Andrarum Limestone and *Micromitra* sp. from Australia was identified, by XRD methods, as carbonate hydroxylapatite in all cases (*M. semicircularis* was also partly silicified).

Amino acids extracted from the apatite of five samples of paterinate shells are listed in Table 1 (p. 240). The simpler neutral amino acids occur as well as the acidic amino acids (D/E) which may have been protected by interaction with apatite as no basic amino acids were detected. The samples of *Micromitra semicircularis* contained the lowest concentration of amino acids; no aspartic acid/asparagine occurred in these samples. The *Dictyonites perforata* specimens contained the highest level of amino acids while their composition differed markedly from those of *Askepasma toddense*, *Micromitra pusilla* and *Micromitra* sp. In these three samples, the level of aspartic acid/asparagine is far greater than that of glutamic acid/glutamine.

The significance of the difference between the amino acid residues of *Dictyonites* and the other paterinates sampled cannot be resolved until current biochemical studies on living and fossil lingulide and discinide shells have been completed. The difference may reflect the greater geological age of the three Cambrian samples compared with that of the middle Ordovician *Dictyonites*. It may even be linked to inherent biochemical changes, like the periodic reduction in phosphatic secretion that gave rise to the perforations of the *Dictyonites* shell.

MORPHOLOGY OF LARVAL SHELLS

The larval shell is a conspicuous feature of the umbones of paterinate valves. It consists of a protegulum, secreted by embryonic epidermis, and a surrounding band, up to 15 μm wide, secreted by the vesicular cells of the circumferential, first-formed outer mantle lobe. This band has been

termed the 'halo' by Chuang (1977) who interpreted the feature as marking the change from a planktotrophic to a sedentary, filter-feeding mode of life. In a fossil, therefore, a halo signals a fundamental change not only in the mode of shell secretion but also in the former life style of the specimen under study.

The paterinid larval valves, defined by halos 9–14 μm wide, are roughly semicircular and c. 600 μm wide with the larger ventral valve as much as 700 μm in *Dictyonites fredriki* (Holmer 1989), (Pl. 12, figs 11–13). The larval shell is also tuberculate (Pl. 7, fig. 1) (Popov *et al.* 1982) except for those of *Dictyonites*, *Lacunites* and *Askepasma*, which are respectively smooth and additionally covered with a periostracum indented by close packed hollows as in mature shells. The micromorphology of the larval shell is variably preserved but that of *Micromitra* appears to be typical of all paterinates except for that of *Dictyonites* which has been described as 'being somewhat porcellaneous' and forming 'hemiconical' apices (Cooper 1956, p.185).

Micromitra *larval shell*

The umbones of some *Micromitra* valves from Turkey are sufficiently well preserved to prompt a reconstruction of the gross anatomy of the larva (Pl. 7, figs 1, 4). The tubercles of both larval valves are hemispherical in the undeformed state, with a diameter of 4·5–6 μm, and were secreted in open hexagonal arrays. The tubercles tend to fade marginally and become more sporadically distributed before dying out on the halo. Exfoliation of the larval shell shows that the tubercles have solid cores (Pl. 7, fig. 2) composed of spherules 150–300 nm in size.
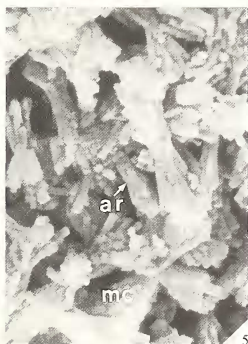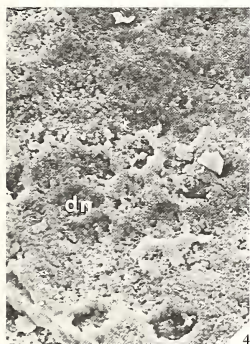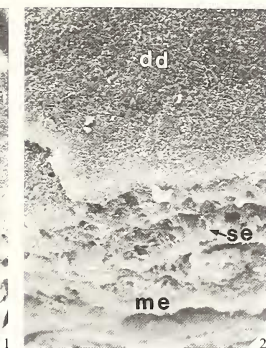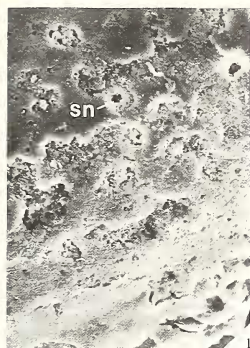
The microtopography of the larval surface indicates that the shell must have been very flexible, presumably reflecting a high organic content. The dorsal valve is inflated into a posteriomedial mound and an arcuate one immediately within the halo (Text-fig. 3A). The latter is divided into four inflated lobes by a medial cleft and a pair of anteriolateral fold systems c. 7 μm wide where they breach the halo (Pl. 7, fig. 3). The valve was evidently secreted before inflation took place so that the tubercles became deformed into strain ellipsoids within fold systems (Pl. 7, fig. 3) and along wrinkles, like those forming transverse creases across the medial mound (Pl. 7, fig. 1). There is no concentric banding within the larval shell apart from the halo which bears traces of subparallel grooves 8–12 μm apart (Pl. 7, fig. 5). These grooves have been interpreted as the casts of intercellular thickening on the basal layer of the periostracum. Their disposition suggests that they are traces of the elongate vesicular cells of a newly differentiated outer mantle lobe.

The larval ventral valve of *Micromitra* is also lobate but the lobes are less well defined and extend anteriorly for no more than 300 μm, well within the halo (Pl. 7, fig. 4; Text-fig. 3B). The lobes are

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PLATE 5

WILLIAMS *et al.*, *Cryptotreta*, *Paterina*?

not complementary to those of the dorsal valve. They are subordinate to a medial sulcus, about 150 μm wide anteriorly, along which the submedial lobes may leave 'growth' tracks as curved grooves forming nick points with a sharp medial groove which may breach a filum or two beyond the ventral halo. A sub-circular depression, about 100 μm in diameter, may also occur near the apex of the umbo. The posteriomedial arc of the ventral halo of *Micromitra* is compressed but still distinguishable along its junction with the apex of the homeodeltidium.

Dictyonites *larval shell*

At first sight, the larval shell of *Dictyonites* (Holmer 1989, fig. 116; Pl. 12, figs 11–13), although comparable in dimensions to that of *Micromitra*, appears to be unique as it lacks tubercles and is distorted by wrinkles within a rigid, hoop-like halo. In fact, the difference between the larval shells of *Dictyonites* and *Micromitra* is due to the shrivelling of the integument of the former genus, which must have been almost entirely organic when first secreted. Both valves are underlain by an apatitic layer which must have been secreted during post-larval growth as an infill of the irregularly shaped, first-formed cover. This break in the secretion of the umbonal successions may account for the absence of tubercles which initially may have been secreted, as discrete domes of apatite, by hexagonally close-packed larval epithelium. Notwithstanding such shrinkage, the medial mound of the dorsal valve with its transverse creases can be recognized as can the four peripheral lobes transformed into collapsed hollows with ridges replacing the anteriolateral fold systems. The submedial lobes separated by a broad sulcus in the larval ventral valve of *Micromitra* can also be identified in *Dictyonites*, with the outer lobes replaced by lateral hollows.

Inferred anatomy of paterinid larva

The paterinid larval shell was evidently flexible enough to form a cast of the main anatomical features of the larva; and we have interpreted its microtopography in the following way.

The halos of both valves are complete although compressed along their posteriomedial arcs (Pl. 7, fig. 6). These arcs delineate an elliptical space between the valves without any trace of their having originated by an equatorial rupture of a circular plate in the manner of the protegulum of living *Lingula* (Yatsu 1902, p. 31) or as two independently developed plate-like valves as in discinids (Chuang 1977, p. 40) and craniids (Nielsen 1991, p. 19). Indeed, the closest analogy is with the larval shell of articulated brachiopods (Percival 1960, p. 447; Stricker and Reed 1985*a*, p. 298; 1985*b*, p. 264).
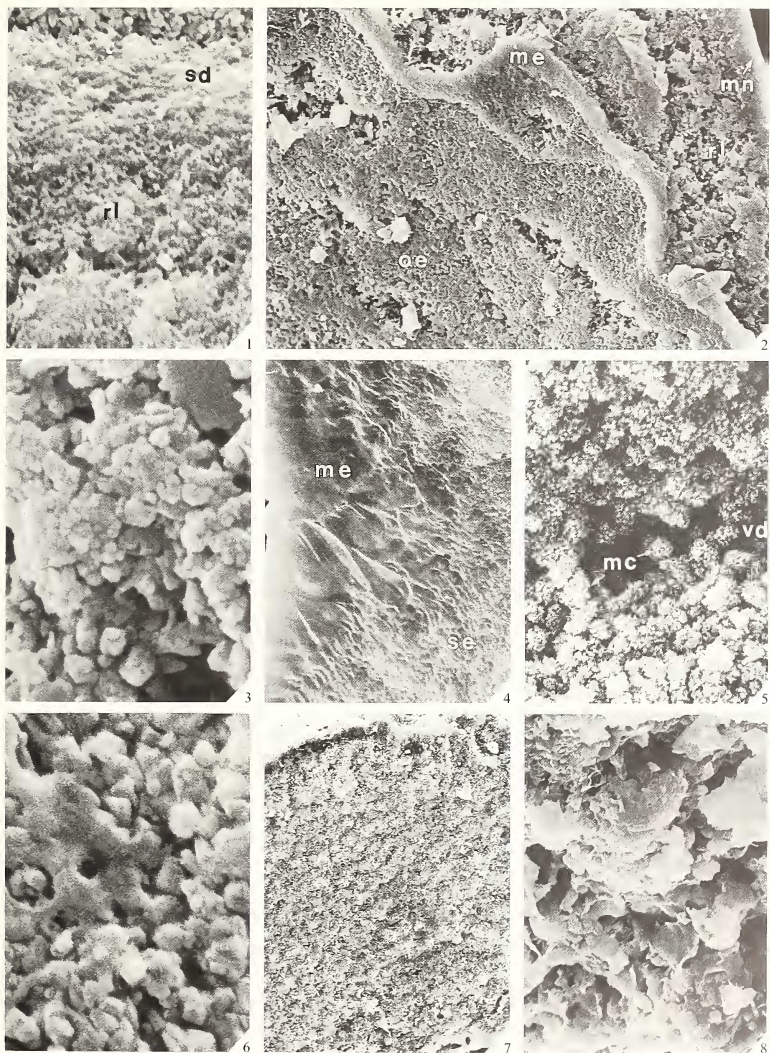

PLATE 6

TABLE 1. Amino acids associated with apatite of fossil paterinates. Amino acid composition expressed as pmole amino acid/mg shell using the one letter code for amino acids where D/N = aspartic acid/asparagine; E/Q = glutamic acid/glutamine; S = serine; G = glycine; T = threonine; A = alanine; Y = tyrosine and V = valine. Values are mean values for duplicate analyses where the maximum error was 6·25 per cent. of mean.

	D/N	E/Q	S	G	T	A	Y	V	Total
Dictyonites perforata	13	45	37	230	29	80	0	30	464
Micromitra semicircularis	0	20	15	100	0	38	41	24	238
Askepasma toddense	119	8	12	93	0	51	4	50	337
Micromitra pusilla	165	14	15	58	0	31	0	23	306
Micromitra sp. (Australia)	166	7	8	52	0	18	26	17	294

On the dorsal valve (Text-fig. 3A), the posteriomedial mound is assumed to have accommodated much of the digestive system, especially the stomach. The fainter, medially placed lobes of the ventral valve (Text-fig. 3B) may represent impressions of a ventral digestive diverticulum as they flank a medial groove which possibly traces the junction of the mesentery with the valve floor. The site and form of the sub-circular depression sporadically indenting the apex of the ventral valve (Text-fig. 3B), suggests that it was an attachment base of myofibrils, possibly associated with a differentiating pedicle.

The bilateral symmetry of the lobes crenulating the halo of the dorsal valve suggests that any features characterizing them should still have functioned at the mantle margins during the transition from a planktotrophic to a sedentary mode of life. Moreover, the indentations, effected by fold systems and median cleft, fade within 60 μm beyond the halo so that any anatomical features giving rise to them were transitory. Larval setae are obvious candidates for such a role; and the symmetry of the lobes suggests that each lobe could have borne a sac containing a set of setae (Text-fig. 3A). Such an arrangement would be consistent with the view that the sacs arose not from mesodermal tissue (Chuang 1977, p. 46) but from thickened ectoderm (Nielsen 1991, p. 9) along the mantle margin.

In comparing this inferred setal arrangement with those of living brachiopods, a distinction has to be drawn between the functionally different embryonic (or larval) setae and mantle setae which appear between the outer and inner mantle lobes. No embryonic setae develop in living lingulids and only one pair occurs in the dorsal valve of *Discinisca* (Chuang 1977). In contrast, the larvae of organocalcitic-shelled craniiforms and rhynchonelliforms are respectively characterized by three pairs (Nielsen 1991, p. 9) and two pairs (Percival 1960, p. 415; Stricker and Reed 1985b, p. 236) of sacs with larval setae in the dorsal valves. The resultant microtopography in living rhynchonelliform species bears some peripheral resemblance to the paterinid pattern (Text-fig. 4).

MORPHOLOGY OF MATURE SHELLS

The morphology of the post-larval paterinate shell is quite variable for such a short-lived group. The functional implications of many of the changes suggest that they were important transformations in paterinate diversification. Three groups of such characters have been used in our analysis of the class. They are changes in: shell shape and ornamentation; the disposition and structure of the posterior margins; markings on valve floors interpreted as imprints of muscle systems, mantle canals and gonadal sacs.

Shell shape and ornamentation

Most paterinates, including *Paterina* (Pl. 11, figs 4–7), *Micromitra* (Pl. 12, figs 9–10) and *Dictyonina*, have a transverse, ventribiconvex, rectimarginate shell. Only the earliest known paterinates are different; *Cryptotreta* is also ventribiconvex but is unisulcate with a gently convex dorsal valve,

while *Aldanotreta* (Pl. 10, figs 1–5) is uniplicate and strongly biconvex. Paterinate shells, although small, are generally large enough to have enclosed spirolophous lophophores and it is not unreasonable to assume that basic variations in shell shape reflected differences in the orientation of spiralia.

The development of strong interareas among paterinates reflected variations in the circumferential expansion of the valves, contrary to Beecher's conclusion (1891, p. 346) that growth was typically hemiperipheral. The shell of most paterinates grew mixoperipherally or holoperipherally, dependant on the attitude of the ventral interarea. Indeed, only the dorsal valves of *Cryptotreta* and *Salanygolina* lack interareas and conform to the hemiperipheral pattern of growth.

Paterinate ornamentation was more conveniently discussed in describing the ultrastructure of the superficial layers of the shell. Distinctive patterns involving radial as well as concentric features, however, have been used to characterize most genera and require further comment.

The pitted coat of the *Askepasma* shell has been interpreted as a lithified periostracum. Traces of lithified periostracum, found on the interarea of *Micromitra* and, less certainly, on the shell of *Dictyonina*, bear no remnants of superstructures or of a moulded basal layer as in *Askepasma*. Apparently all paterinate periostraca, except that of *Askepasma*, consisted essentially of a sheet-like basal layer.

Ribs are rarely developed in paterinates. *Cryptotreta* and *Aldanotreta* are usually described as finely capillate and *Micromitra* is normally regarded as having low, discontinuous costellae. Many of these 'capillae' and 'costellae', however, break the concentric ornamentation into drapes (Pl. 10, fig. 8) and are effectively traces of radially successive nick points (Williams and Holmer 1992).

Concentric ornamentation is prevalent among paterinates and, as already shown, evolved into offset arrays of depressions. Fine, concentric fila are characteristic of cryptotretids, *Askepasma* and *Paterina*. In the latter genus they are commonly broken into drapes by radial sets of nick points (Pl. 14, fig. 4). The close-packed depressions of *Micromitra*, *Dictyonina*, *Dictyonites* and related genera (Pl. 12, figs 7–13), on the other hand, are homologous and originate as off-setting, concave arcs of asymmetrical fila.

Posterior margins

The posterior margins of paterinate valves are among the most distinctive features of the class. Laterally they are the commissures of strophic cardinal areas that were contiguous in the living state (Rowell 1980). These areas have previously been identified as 'pseudointerareas' on the assumption that they were secreted by discrete posterior mantle lobes. As will be shown, however, they are homologous with the strophic 'interareas' of the older rhynchonelliforms. We have, therefore, identified the paterinate cardinal areas as interareas throughout this paper. Medially, the interareas define the relatively large openings of the delthyrium and notothyrium (Pl. 12, figs 2–3), which may be variably covered or restricted by a homeodeltidium and homeochilidium. The ultrastructure of the margins of *Askepasma* is most easily understood as the pitted periostracum of this genus also covered the larval shell; and its easily recognized boundaries trace the epithelial junctions along the edges of the interareas and a delthyrium lacking a homodeltidium.

Askepasma *posterior margin.* In the apical angle of the delthyrium (Pl. 8, fig. 1), an arc of periostracum, delineating the posterior margin of the larval ventral valve of *Askepasma*, is inwardly succeeded by ten or more arcuate phosphatized membranes intercalated with recrystallized, spherular apatitic laminae with some clay (Pl. 8, fig. 3). These stratified laminae pass anteriolaterally into a smooth ledge of shell with a curved face, which underlies the periostracum of the ventral interarea (Pl. 8, figs 1–2, 4).

The relationship between the periostracum of the ventral interarea underlain by apical stratified laminae and the apatitic ledge is intricate. The interarea consists of a succession of concentric folds, *c.* 40 μm in wavelength, parallel with the posteriolateral commissure (Pl. 8, fig. 1). The folds are covered with periostracum deflected as a series of en échelon folds which, together with the shell

ledge, form the anteriolateral margins of the delthyrium (Pl. 8, fig. 2); an arrangement interpreted as follows. The periostracum, underlain by stratified laminae, traces the junction between the outer epithelium, responsible for the secretion of periostracum with stratified laminae, and unfossilized 'pedicle' epithelium. An exhaustive review of relevant micrographs prepared by Professor H. B. Whittington (1980) showing the attachment of *Dictyonina* to the sponge *Choia* and of impressions of *Dictyonina* in the Burgess Shale purporting to show a pedicle, revealed that the holdfast was not an appendage like those of living brachiopods. It was probably a patch of thickened epithelium differentiated to secrete an adhesive polymer through 'rootlets' and, therefore, cytologically comparable to the microvillous epithelium at the pedicle tips of living linguloids (MacKay and Hewitt 1978).

In accordance with processes of integumentary differentiation throughout the phylum, the pedicle epithelium presumably would have been confined to a sub-circular patch coincident with the delthyrial and notothyrial margins of the larval shell. The shell ledges of the ventral interarea would have been secreted by the ventral outer mantle lobe; and the loci, where the ledges on either side of the delthyrium pass into the posteriomedial arc of stratified laminae, would have marked the intersection of the trace of this ventral outer mantle lobe with the sub-circular patch of pedicle epithelium (cf. Pl. 8, fig. 4).
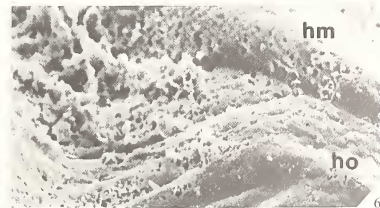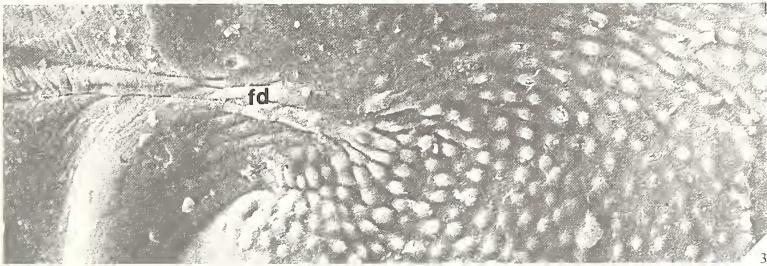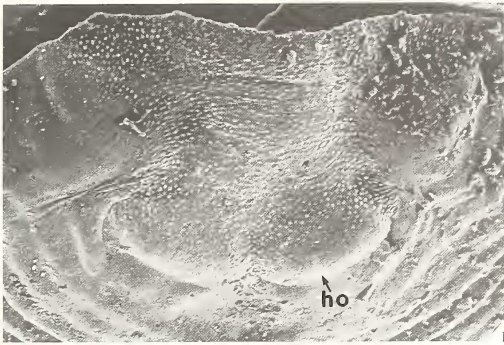
The posterior margin of the dorsal valve is also a smooth, rounded ledge of shell, composed of compacted apatitic spherules (20 nm or so) and facing ventrally from beneath the periostracum-covered bands of the interarea. Even the best preserved ledge available for study bore no articulatory devices, only traces of shallow grooves, *c*. 1·5 μm wide and up to 15 μm apart and subtended at acute angles towards the lateral margins of the interarea (Pl. 8, fig. 5). The ledge, however, did bear traces of periostracum well below its external edge (Pl. 8, fig. 6). A concave plate at the notothyrial apex (Pl. 8, fig. 7) which may have been identified previously as a homeochilidium is similar to the dorsal 'muscle platform' of *Micromitra* described below.

The pedicle/outer epithelial junction, identified in the ventral valve, has not been found in the dorsal valve either because it atrophied during ontogeny or because it never impinged upon the larval dorsal valve. However, the dorsal interarea was secreted by the outer mantle lobe in the same way as its ventral counterpart. As for their secretion and contiguity, the interareas of *Askepasma* would have been similar to the interareas of strophic articulated brachiopods. This assumption is consistent with the presence of incomplete setal fringes around several shells of Burgess Shale *Dictyonina* but not along their posterior margins (Whittington 1980; pers. obs. by LEH and LEP). Even so, the inferred arrangement of epidermis within the posteriomedial part of the shell, favours the existence of a posterior body wall like that of all inarticulated brachiopods if only to accommodate an anus (Text-fig. 5).

Micromitra *posterior margin*. The inferred differentiation of the epidermis along the posterior margins of paterinates with homeodeltidia has to be different from that of *Askepasma* (Text-fig. 5).

PLATE 7

WILLIAMS *et al.*, *Micromitra, Dictyonites*

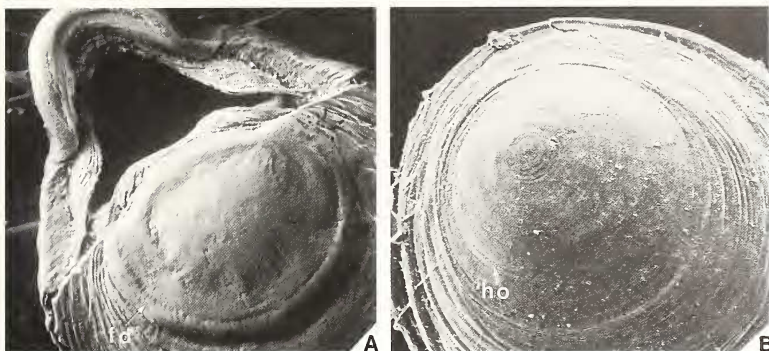TEXT-FIG. 3. The inferred dorsal (A) and ventral (B) views of the gross anatomy of the larva of *Micromitra*, based on the micromorphology of valves of *M.* cf. *ornatella* from Turkey (compare Pl. 7, figs 1, 4).

TEXT-FIG. 4. Dorsal views of immature shells. A, 'young' terebratulide with anteriolateral folds (fd) affecting the larval dorsal valve; from intertidal sands, Connemara, Ireland; ×37. B, *Discinisca tenuis* with an undeformed halo (ho) defining the larval dorsal valve; from a washed up cluster of shells at high water mark, Swakopmund, Namibia; ×90.

The homeodeltidium of *Micromitra* is only incipiently developed in young post-larval shells. In mature valves, however, it can be a large, semi-conical structure, well over 1 mm in diameter at the dorsal margin (Pl. 9, fig. 1). The feature evidently grew as an integral part of the ventral interarea because, rarely, well preserved bands of lithified periostracum, commonly disposed as en échelon folds up to 7 μm in wavelength (Pl. 9, figs 2–4), can be traced from the interarea on to the homeodeltidium (Pl. 9, fig. 1). In effect, the periostracum and underlying apatitic shell, along the dorsal ledge of the homeodeltidium, must have been secreted by the medial segment of a continuous outer mantle lobe controlling the growth of the ventral interarea.

Such realignment could have affected the location of the pedicle base in two ways. Firstly, the growth of the homeodeltidium may have been in phase with the atrophy of the pedicle. This is unlikely as specimens of the homeodeltidium-bearing *Dictyonina* found in the Burgess Shale are attached to their substrates although not by any discernible appendage. Accordingly, the more feasible assumption is that attachment was effected by a patch of adhesive pedicle epithelium which had been differentiated out of the posterior body wall (inner epithelium) as in *Lingula* and which had migrated dorsally at the edge of the growing homeodeltidium.

Posterior margins of other paterinates. Genera assigned to the Paterinidae are invariably characterized by having flattened interareas in both valves divided by widely triangular delthyria and notothyria.

As in *Askepasma*, the delthyrium of *Paterina* is open (Pl. 12, figs 2–3) but in other paterinids homeodeltidia are variably developed intragenerically as well as ontogenetically. In *Dictyonina*, a homeodeltidium is present in some species and appeared late in ontogeny. The homeodeltidium of *Micromitra* is also formed late, being vestigial in juvenile valves; whereas those of *Dictyonites*, *Lacunites* and, possibly, *Kolihium* were present in juvenile valves and developed strongly during subsequent growth. The development of the homeodeltidium can be correlated with the attitude of the ventral interarea relative to the commissural plane. Paterinates with an open delthyrium and vestigial homeodeltidium invariably have an apsacline ventral interarea; while homeodeltidia of species with procline to slightly cataline interareas are well developed and extend posteriorly to the commissural plane.

The development of a homeochilidium over the dorsal notothyrium is rare. Homeochilidia have been described in some paterinids and even used as a generic diagnostic character. However, only *Askepasma* has a true homeochilidium; and the structure so identified in other paterinids is the thickened outer margin of a median plate. This concave, transverse median plate may overhang the valve interior as in *Micromitra* (Pl. 11, figs 2, 9–10) or be supported by secondary shell. There is some evidence to suggest that muscle bases were inserted on the median plate. That of *Micromitra* sp. from Argentina bears shallow, hexagonally packed pits, like those found on the valve floor within an area presumably occupied by muscle bases (Pl. 11, figs 1, 3). In well preserved *Paterina* from Australia, the median plate is indented by a pair of sub-circular depressions, separated by a pair of submedial ridges dying out posteriorly and contained anteriorly by an arc of five low tubercles (Pl. 9, figs 5–6). These impressions have been interpreted as the insertion areas of the dorsal ends of 'diductor' muscles.
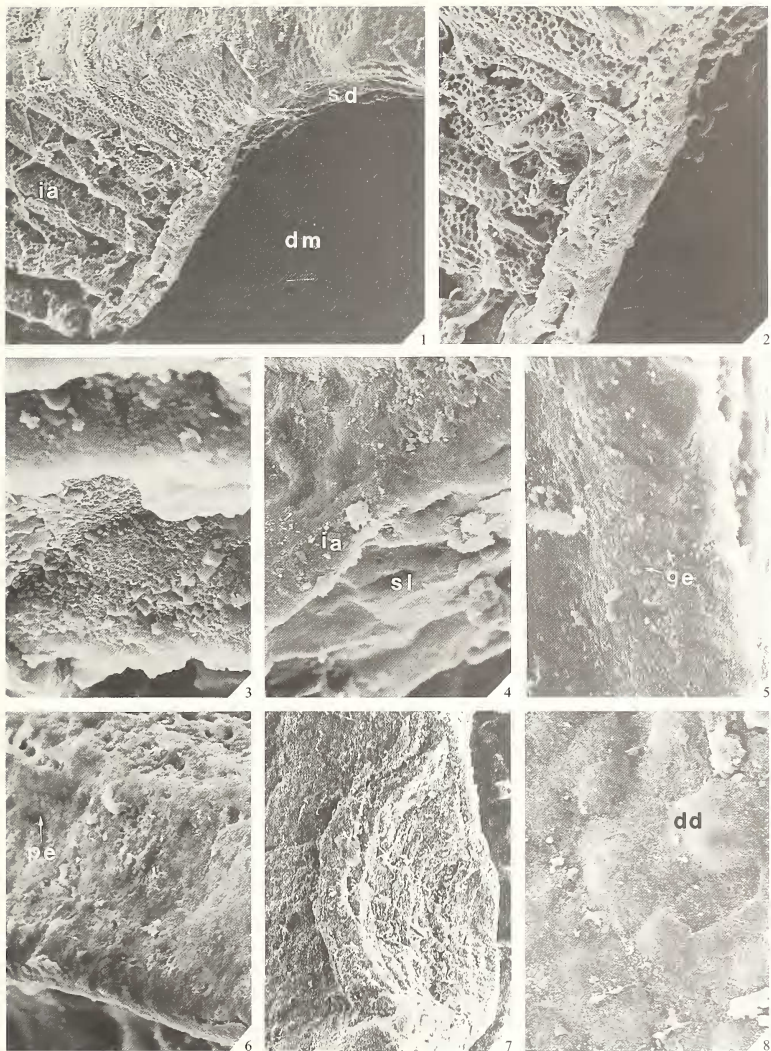
The posterior margins of cryptotretids are different from those of the paterinids. In *Aldanotreta*, the ventral interarea is flat, apsacline, and divided by a triangular delthyrium (Pl. 10, fig. 2); the dorsal interarea forms a high, flat, undivided plate (Pl. 10, fig. 5). In *Cryptotreta* and *Salanygolina*, the ventral interarea forms a high, triangular plate divided by a narrow, ridge-like homeodeltidium completely covering the delthyrium. Illustrations of the ventral valves of these two genera suggest that the growth of homeodeltidia and interareas were always in phase as there are no deflections of growth lines along the entire lateral margins of the homeodeltidia. It seems possible, therefore, that a true delthyrium was not developed in these two genera. The inclination of the ventral interarea is apsacline in *Salanygolina* (Ushatinskaya 1987, pl. 7, figs 5, 9), but almost orthocline in *Cryptotreta* (Pelman 1977, pl. 21, fig. 3; pl. 22, fig. 1). The genera also lack dorsal interareas (Pelman 1977, pl. 21, fig. 2; Ushatinskaya 1987, pl. 7, figs 8–9); and their wide, straight posterior margins were formed by hemiperipheral growth. In her original description, Ushatinskaya (1987) identified a vestigial dorsal interarea and chilidium in *Salanygolina*; but published illustrations, and examination of the type specimens suggest that the shell margin is merely thickened where a slightly raised muscle field might have been situated. In this respect, *Salanygolina* is similar to brachiopods of the calcitic-shelled *Chileida* (Popov and Tikhonov 1990).

Several features of the paterinate posterior margins still have to be explained in the context of such a 'migrating' pedicle base. A convex biomineralized cover of the delthyrium of living brachiopods, resembling a homeodeltidium, accommodates the capsule of a differentiated pedicle (some terebratulides) or a posteriomedial muscle system (thecideidines). As there is no evidence of a differentiated pedicle, the paterinide pedicle could have been attached to the apex of the ventral valve by a strip of myofibrils. It is therefore possible that the homeodeltidium (and a postulated cuticular arch in paterinates with an open delthyrium) covered posteriomedial muscle systems, especially primitive diductors responsible for the opening of the valves.

The contiguity of the strophic margins of the interareas, as seen in well preserved paterinate shells (Rowell 1980), has to be reconciled with the absence of posterior setae (as in the Burgess Shale

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PLATE 8

WILLIAMS *et al.*, *Askepasma*

TEXT-FIG. 5. Diagrammatic representation of the inferred structural relationships between mantle, pedicle and the ventral and dorsal interareas of a paterinid with a well-developed homeodeltidium.

Dictyonina) and of biomineralized articulatory devices. Among living species, the setal fringe is complete in disarticulated lingulates but absent from the posterior margins of articulated rhynchonelliforms (the cemented inarticulated craniids and articulated thecideidines have no setae). The absence of setae along the hinge lines of living rhynchonelliforms results from the fusion of the outer mantle lobes underlying the interareas (Williams 1956). These fused mantle lobes continue to secrete, from a shared slot defined by lobate cells, thickened periostracal sheets as covers for both interareas (Williams and Hewitt 1977).

Despite investigations by Bell (1941) and others, no convincing articulating devices have yet been found in paterinates. Even microscopic features of an interlocking nature are absent. The oblique grooves found on the dorsal commissure of *Askepasma* (Pl. 8, fig. 5) could conceivably represent traces of the folding characteristic of the periostracum on interareas (cf. Pl. 9, fig. 2). However, they are too random to represent an organized device.

In the face of these data and assumptions, we conclude that living paterinates functioned as articulated brachiopods, pivoting on the lateral edges of their interareas (Text-fig. 5). Medially, the shell was probably held together by a muscle system (including diductors) and an overlying posterior body wall and pedicle base. The body wall, being exposed, was probably ciliated (unlike the inner mantle lobes) and partly protected by a glycocalyx of multi-layered pellicles as in living discinoids. It may also have contained the anal opening had the gut been orientated like that of the craniids. Lateral of the delthyrium and notothyrium, the shell would have been hinged by the periostracal covers of both interareas. These periostracal sheets would have been secreted from a common groove within fused outer mantle lobes and would have been thickened into two sets of en échelon folds (cf. Pl. 9, figs 2, 4; Text-fig. 5) disposed at acute angles to the axis of valve rotation. Traces of periostracum along the commissures of *Askepasma*, well below the external edges of both contiguous interareal margins (Pl. 8, fig. 6), support the existence of such a common groove.

Internal impressions

Soft part attachments are difficult to discern in paterinates except for some species of *Paterina*, *Dictyonina* and *Micromitra*. In these three genera, the small ventral body area occupied the posteriomedial sector of the valve just in front of the delthyrial opening; the dorsal body area was larger as it included the anteriorly spreading muscle field.

Muscle systems. There are traces of two paired (posteriomedial and anteriolateral) muscle fields on the floor of the ventral valve (Pl. 11, figs 6–7; Text-fig. 6). They are probably composite scars that served as attachment areas for several different groups of muscles, although their components are difficult to recognize. The anterior and lateral boundaries of the posteriomedial muscle fields are a pair of thick ridges along the delthyrial margins and the attachment areas are invariably extended on to the inner sides of the homeodeltidium. In *Paterina*, which has an open delthyrium, the ridges form a pair of strongly thickened plates converging onto the valve floor. The paired ventral anteriolateral muscle fields are situated on the thickened parts of the valve floor (Pl. 11, figs 6–7), anteriolateral of the delthyrial margins possibly in association with gonadal ties (Text-fig. 6). They seem to be composite scars as at least two components can be recognized in well preserved specimens. In *Askepasma* and some species of *Micromitra*, a pair of low submedial ridges bisect the ventral body area (Pl. 11, fig. 11).

The body areas of paterinid dorsal valves are dominated by four large, radially arranged, slightly raised muscle tracks. (Pl. 11, figs 2, 9–10; Text-fig. 6). These tracks lie forward of the median plate within the notothyrium, on either side of a sporadically developed fine medial ridge. The plate is supported by a pair of submedial ridges which are strongly thickened and raised posteriorly in some species (Pl. 11, figs 9–10). A pair of circular depressions, presumably muscle bases, has been found on the medial plate of a dorsal valve of the Australian *Micromitra* (Pl. 9, figs 5–6).

Any reconstruction of a paterinid muscle system, consistent with inferred scars of attachment, is necessarily speculative. Speculation, however, has to be conducted within certain constraints (Rowell 1980). In particular, posteriomedial impressions, interpreted as muscle bases, and the contiguity of strophic interareas suggest that the valves operated on a lever system. The simplest one would have been a first order leverage, as in most articulated brachiopods, about a periostracal hinge axis as described above. Such a muscle system would have involved diductors and adductors in the following way. The anteriolateral ventral scars, possibly including gonadal ties (Text-fig. 6), and the rarely preserved scars on the dorsal plate (or the raised notothyrial platform of *Askepasma*),

could have been the respective attachment areas of the ventral and dorsal ends of diductor muscles. In complement, the two pairs of radial muscle tracks in the dorsal valve and the paired posteriormedial muscle fields, located on the inner side of the delthyrial ridges and of the homeodeltidium (and the large umbonal scar of *Askepasma*), in the ventral valve, could have been attachment areas for adductor muscles (Text-fig. 6).

The paterinate musculature interpreted in this way is overtly articulate in arrangement. However, if the paterinates are linguliforms, it is possible that the adductor muscles of paterinates are homologous with the posterior adductors of the discinoids (Williams and Rowell 1965, fig. H29). Alternatively, the paterinid diductors could correspond to the posterior adductors of discinoids (and the umbonal muscles of linguloids); and the paterinid adductor muscles with the anterior adductors and oblique laterals of discinoids. Finally, a correlation could even be effected with the muscle system of craniiforms with the paterinid diductors being homologous with the posterior adductors of craniid and the adductors with the anterior adductors and oblique internal muscles of *Neocrania*.
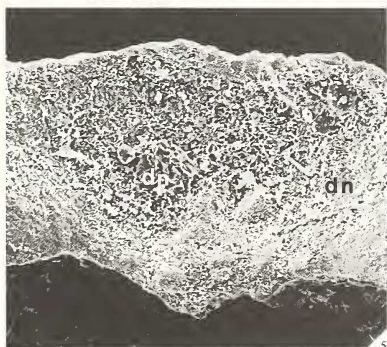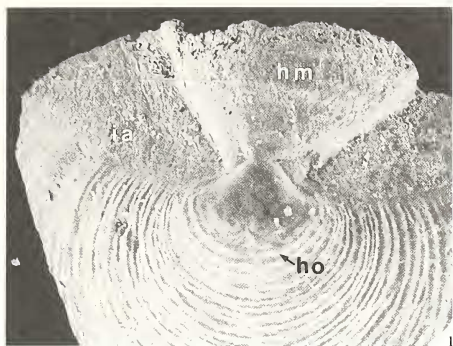
Notwithstanding these various interpretations of paterinate musculature, the general arrangement of adductor scars is rather conservative in all known Early Palaeozoic brachiopods except the lingulides. Indeed, it is likely that the posterior and anterior adductors of discinids, craniiforms and rhynchonelliforms are homologous; and that some of the oblique muscle scars in trimerellides, obolellides and rhynchonellates functioned like diductors (Gorjansky and Popov 1986; Popov 1992). It is, therefore, probable that the adductor scars of paterinates and other contemporaneous brachiopods are homologous. The paterinate muscle system, identified as 'diductor', almost certainly evolved from some kind of oblique musculature. Their precise homology with various oblique muscles in lingulates and craniiforms, or with the diductors of rhynchonelliforms, however, remains uncertain.

Mantle canals. A paterinate mantle canal system was first described by Laurie (1986, 1987) who identified saccate mantle canals in both valves of *Paterina*. Saccate mantle canals are also characteristic of both valves of *Dictyonina* and *Micromitra*. Pinnate mantle canals have been observed in the ventral valve of *Askepasma* but the dorsal mantle canal system remains unknown. Traces of pinnate canals have been found in both valves of *Aldanotreta*? *phillipsii* (Holl) (Pl. 10, fig. 6) from the Lower Cambrian of England.

In all mantle canal systems impressed on paterinate shells, traces of peripheral *vascula terminalia* are present and were probably connected with setal follicles in life (Pl. 10, figs 6, 10; Pl. 11, figs 9–10; Text-fig. 6). Laurie (1987) speculated that the saccate mantle canals of paterinids may have accommodated the gonads in proximal sinuses as in rhynchonelliform brachiopods. It is noteworthy that in the interiors of two mature valves of *Askepasma* and *Micromitra* the area supposedly occupied by a gonadal sinus is finely nodular with low domes up to 15 μm in diameter (Pl. 8, fig. 8). This microtopography is common in areas of the shell floor underlying gonads.

PLATE 9

CONCLUSIONS

The new information on the chemico-structure and morphology of the paterinate shell has been used in a phylogenetic analysis of the class. The result is a refinement of the classification of paterinates as a whole and of their phylogenetic relationships with other brachiopods, as presently understood (Williams *et al.* 1996).

Classification of paterinate brachiopods

A phylogenetic analysis of the paterinates, in which character polarity (Appendix 1) is determined by outgroup methods, has to take into account stratigraphical and palaeobiological aspects of brachiopod evolution.

The paterinates include the oldest brachiopods yet recorded, the Tommotian cryptotretids. However, rhynchonelliform, as well as other linguliform brachiopods, are not significantly younger and could well have included the sister group of paterinates. It is, therefore, defensible to use chronostratigraphically appropriate representatives of both subphyla as outgroups for the analysis.

The choice of outgroups has to allow for the fundamental contradictions of the paterinate shell – its organophosphatic composition and its strophic hinge axis – which are mutually exclusive synapomorphies of lingulate and rhynchonelliform brachiopods. The Early to Mid Cambrian genera, *Eoobolus, Fossuliella* and *Botsfordia* and the Mid Cambrian to early Ordovician *Obolus* represent the full diversity of penecontemporaneous organophosphatic lingulides. In particular, they typify the most significant variations in the larval shell, periostracal micro-ornamentation, skeletal ultrastructure and muscle systems of Early Palaeozoic lingulides.

The earliest recorded rhynchonelliforms, all with strophic hinge axes and organocalcitic shells, are the Atdabanian chileates, kutorginates, protorthides and obolellates. The chileates (e.g. *Chile*) are currently placed close to the base of rhynchonelliform clade. In addition to the strophic hinge line, *Chile* resembles Early Cambrian cryptotretids in the hemiperipheral growth of the dorsal valve, the pinnate ventral mantle canal system; and additionally, like the cryptotretid *Salanygolina*, in having a ventral umbonal perforation enlarged by resorption. The kutorginates (*Kutorgina*) and protorthides (*Glyptoria*) are the earliest known rhynchonelliforms with primitive articulatory structures and diductor muscle scars. They are also similar to early paterinides in the morphology of their interareas, delthyrial openings, mantle canal systems and the arrangement of the dorsal adductor scars. The obolellates are the oldest known rhynchonelliforms but are not represented among the outgroups because the earliest known genera (*Obolella, Bicia, Alisina,* etc.) are characterized by many apomorphic features indicative of a derived stock.

PLATE 10

WILLIAMS *et al.*, paterinate brachiopods

In total, seven lingulide and rhynchonelliform genera have been used as outgroups for the phylogenetic analysis of the paterinates. An analysis of the resultant matrix of 17 genera defined by 39 character states (Appendix 2) gave rise to 30 equally parsimonious trees with a consistency index of 0·77. The consensus cladogram (Text-fig. 7) confirms linguliform monophyly, characterized by the synapomorphies of an organophosphatic shell with stratiform lamination and halos delineating the valves of planktotrophic larvae.

Within the Linguliformea, the Paterinata constitute a sister stock of the Lingulata and can be distinguished by such apomorphies as a concentric ornamentation of fila, the posteriomedial locations of ventral muscle fields and radially arranged, dorsal adductor scars. The two families of the class, Cryptotretidae and Paterinidae, are also monophyletic and form two well-defined subclades.

The cryptotretids are the oldest group of brachiopods yet recorded and are distinguishable by such synapomorphies as a periostracum indented by hexagonal pits and a stratiform shell succession dominated by imprinted membranes. Their radiation probably took place early in the Tommotian, as *Aldanotreta* and *Cryptotreta* occur in Tommotian successions and *Askepasma* in the Atdabanian.

Although cryptotretids became extinct before the end of the Early Cambrian, they are remarkably diverse in shell morphology. Synapomorphies include: a folded anterior commissure (uniplicate in *Aldanotreta* and unisulcate in *Cryptotreta*) and a narrow, ridge-like pseudodeltidium in *Cryptotreta* and *Salanygolina*. These features are unknown in other linguliforms, but do occur in some early rhynchonelliforms. Accordingly, some features, identified as apomorphies, may represent plesiomorphies that persisted in some cryptotretids, but were lost in all other paterinates. In particular, the hemiperipheral growth of the dorsal valve and the absence of a dorsal interarea and notothyrium may not be synapomorphies of *Cryptotreta* and *Salanygolina* but plesiomorphies of all brachiopods. Thus they occur in chileates as does a ventral umbonal perforation enlarged by resorption, which, in the paterinates, is also uniquely characteristic of *Salanygolina*.

The paterinids are distinguished in the analysis by many synapomorphies including: the tuberculate micro-ornamentation and lobation of the larval shell; the acquisition of the dorsal median plate (with muscle scars) commonly supported by submedial ridges, a baculate ventral mantle canal system, and strongly thickened inner delthyrial margins. *Paterina* and *Micromitra* are

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Figs 1–3. *Micromitra* sp.; CEGH-UNC 15975; Middle Cambrian (Los Sombreros Formation), Argentina; dorsal valve. 1, surface of median plate; × 161. 2, interior showing radially arranged posterior and anterior adductor scars; × 21. 3, oblique posterior view of median plate and interarea; × 18.

Fig. 4. *Paterina alaica* Imanaliev and Pelman; PM Kg6; Middle Cambrian (Karagaily Formation), Kirgizia; ventral valve interior, oblique anterior view showing strong ridges (rd) developed on lateral sides of delthyrium; × 28.

Fig. 5. *Paterina labradorica* (Billings); USNM 494533 (collection of Bell and Barnes); Lower Cambrian, Labrador; ventral valve interior, oblique lateral view showing strong ridges (dr) on lateral sides of open delthyrium, and position of the posteromedial muscle field (pm); × 18.

Figs 6–7. *Paterina* sp.; USNM 494539 (collection of Bell and Barnes); Middle Cambrian (Grove Crick Limestone), United States. 6, ventral valve interior showing position of posteriomedian muscle fields (pm), thickened anterolateral muscle fields outside of dlthyrial ridges (am); × 9. 7, oblique posterior view of ventral interior; × 12·5.

Figs 8–10. *Micromitra* sp.; CPC 34421; Lower Cambrian (Todd River Dolomite), Australia; dorsal valve. 8, posterior view showing notothyrium (no), interarea (ia) and larval valve (ho); × 179. 9, interior showing radially arranged adductor scars; × 14. 10, oblique lateral view showing position of adductor (aa) and diductor (dd) scars, median ridge (mr) submedian ridges (sr), saccate mantle canals and vascula terminalia (vt); × 17.

Fig. 11. *Askepasma toddense* Laurie; CPC34420; Lower Cambrian (Todd River Dolomite), Australia; oblique posterior view of the ventral valve interior; × 24.

PLATE 11
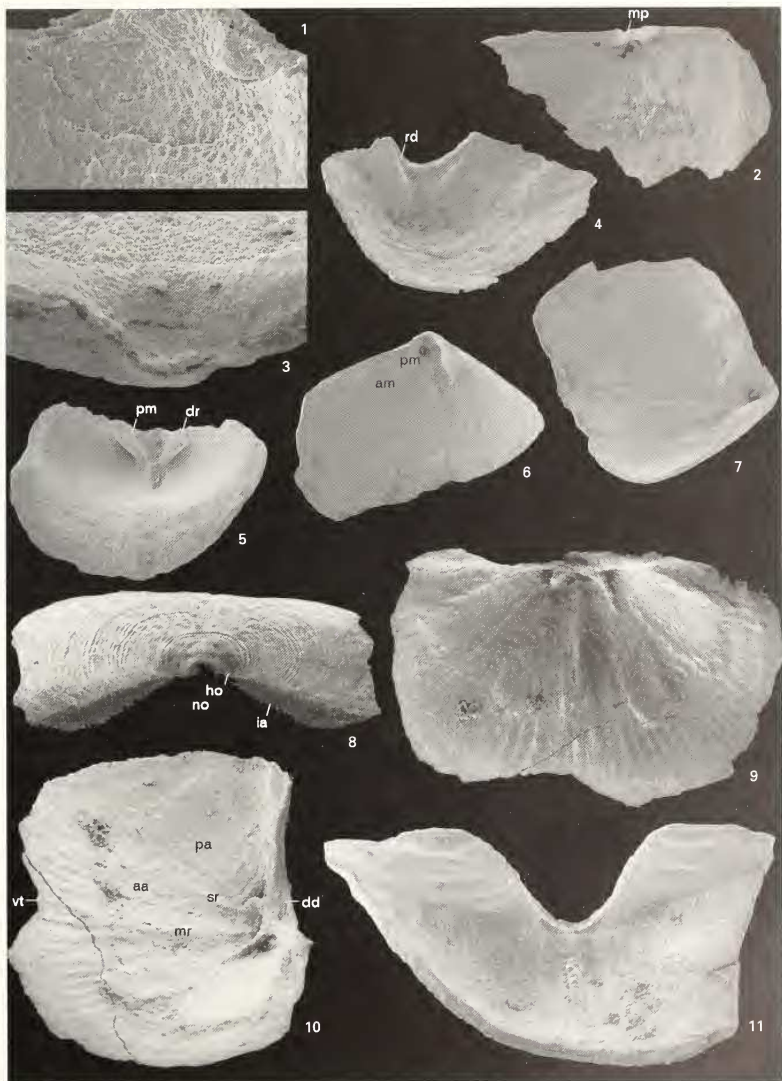
WILLIAMS *et al.*, paterinate brachiopods

apparently the oldest known paterinids, making their first appearance sometime in the Atdabanian. *Paterina* is possibly closest to the ancestral stock of the family, whereas *Micromitra*, *Dictyonina*, *Dictyonites*, *Lacunites* and *Kolihium* possess such plesiomorphic features as: asymmetrical fila with wrinkled outer faces, a broad, convex homeodeltidium, and a saccate dorsal mantle canal system. It is noteworthy that *Dictyonina*, *Dictyonites*, *Lacunites* and *Kolihium* are confirmed as the most derived paterinate group by the progressive complexity of their offset depressions in the postlarval shell. This assumption is supported by their stratigraphical record. *Dictyonina* makes its first appearance in the uppermost Toyonian Stage of the Lower Cambrian, *Lacunites* is known from the upper Middle Cambrian, whereas *Dictyonites* and *Kolihium* are restricted to the Ordovician.
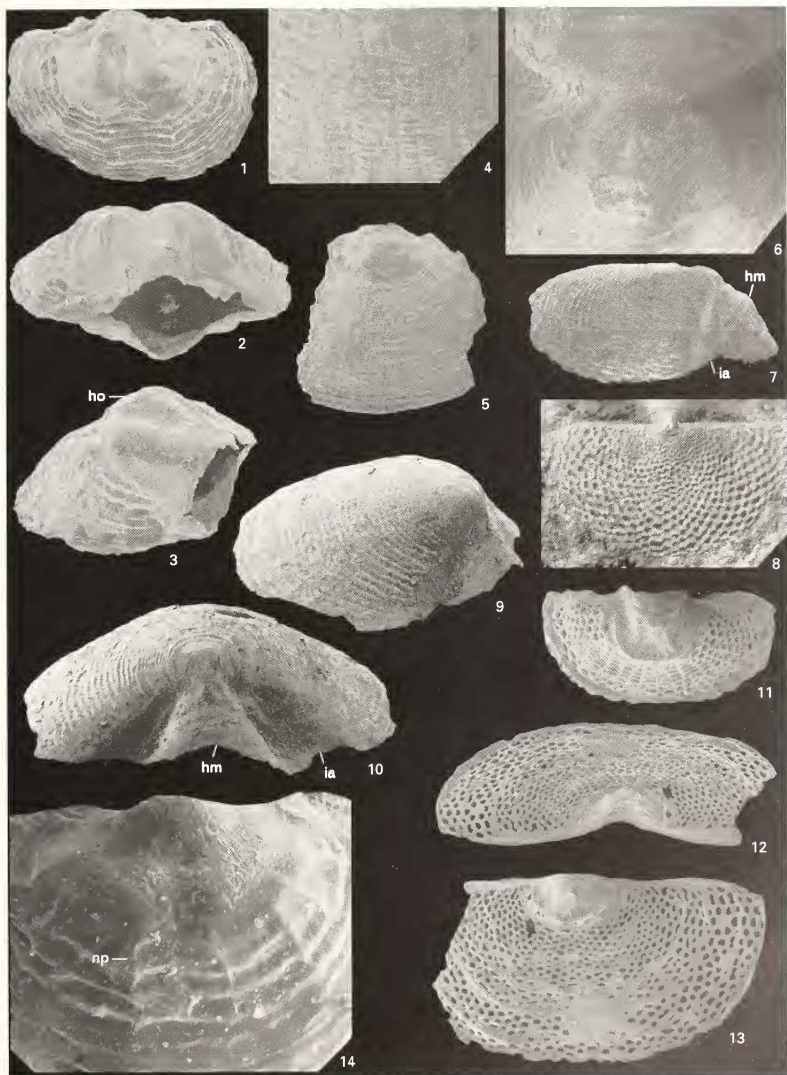
Affinities of paterinate brachiopods

Our present perception of paterinate phylogeny is based on data derived exclusively from the shell. The data, however, allow some inferences to be drawn on the anatomical and ontogenetic differentiation of the class during the early evolution of the phylum. The initial separation of the paterinates from the main brachiopod lineage(s) probably took place just after the divergence of the major clades of organophosphatic linguliforms and calcitic craniiforms and rhynchonelliforms. It is also possible that paterinates retained many plesiomorphic characters that persisted from the brachiopod stem group. We assume that such features include: the peripheral bifurcation of the *vascula terminalia*; a body wall with vestigial musculature; mantle lobes joined posteriorly by a strip of inner epithelium (body wall); and attachment to the substrate by a chitin-covered outgrowth (pedicle) of the posterior body wall. These plesiomorphies also persisted in some rhynchonelliform stocks. Thus, nearly all the characters listed above typify the chileates which feasibly represent the most primitive rhynchonelliforms (Williams *et al.* 1996).

The subsequent radiation of organophosphatic brachiopods is presently seen as involving the emergence of the paterinates and lingulates as sister groups. Yet the earliest paterinates, the cryptotretids, could have been descendants of a short-lived lineage that evolved directly from the brachiopod stem group (or the basal linguliform stock). Our analysis also suggests that many so-called linguliform features are, in reality, apomorphies that arose within the lingulates after their

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EXPLANATION OF PLATE 12

Figs 1–3. *Paterina alaica* Imanaliev and Pelman; Pm Kg5; Middle Cambrian (Karagaily Formation), Kirgizia; complete juvenile specimen. 1, ventral view; × 66. 2, posterior view; × 73. 3, oblique lateral view showing lobate larval shell (ho); × 73.

Fig. 4. *Paterina* sp.; USNM 494536 (collection of Bell and Barnes); Middle Cambrian (Grove Crick Limestone), United States; ventral valve surface ornamentation; × 103.

Fig. 5. *Micromitra* cf. *modesta* (Lochman); USNM, specimen lost during photography; Upper Cambrian (Elvinia Zone), Nevada; ventral valve exterior showing drapes and fine radial ribs formed by nick points; × 23.

Figs 6–7. *Lacunites alimbeticus* (Andreeva); PM url; lower Ordovician, Arenig (Kuragan Formation), South Urals. 6, umbonal area of ventral valve showing smooth larval valve; × 287. 7, lateral view showing differences in the surface ornament of homeodeltidium (hm) and catacline ventral interarea (ia); × 10.

Fig. 8. *Lacunites balashovae* Gorjansky; CNIGR 247/9960; lower Ordovician, Arenig (Billington Stage), north-western Russia; ventral valve exterior of holotype, showing coarsely pitted post-larval shell; × 6.

Figs 9–10. *Micromitra* sp.; CPC 34422; Lower Cambrian (Todd River Dolomite), Australia; ventral valve. 9, lateral view; × 15. 10, posterior view showing interarea and well-developed homeodeltidium (hm); × 15

Figs 11–13. *Dictyonites fredriki* Holmer; middle Ordovician (Furudal Limestone), Dalarna, Sweden. 11, RM Br128493; ventral view; × 23. 12–13, RM Br128495, holotype. 12, posterior view of dorsal valve. 13, dorsal view. Both × 23.

Fig. 14. *Dictyonina hexagona* (Bell); IGNA437/410; Middle Cambrian, Amgian, Kazakhstan; dorsal valve, umbonal area showing drapes and nick points (np) on the periphery of larval valve; × 135.

PLATE 12

WILLIAMS *et al.*, paterinate brachiopods

TEXT-FIG. 6. Generalized schematic illustration of the ventral (A) and dorsal (B) interiors of *Micromitra* based on the study of several species from Australia and Kazakhstan.

TEXT-FIG. 7. A 50 per cent. majority rule consensus of 30 trees derived in a heuristic search of ten paternate and seven other brachiopod taxa superimposed on a chart with the faint lines representing series boundaries; the known stratigraphical distribution is indicated by black bars.

separation from the paternates. These apomorphies include: a muscular body wall used for the hydraulic opening of the shell, and a highly specialized pedicle developing as a muscular stalk with a coelomic core.

The origin of many basic features of the brachiopod shell has yet to be determined, especially valve articulation. The development of living craniids has been interpreted by Nielsen (1991, p. 25)

as confirming these inarticulated, calcitic-shelled brachiopods as a sister group to living rhynchonelliforms. On this assumption, inarticulation is polyphyletic with the separation of dorsal and ventral mantle lobes of adults developing independently in lingulates and craniates. On the other hand, genetic evidence has prompted Cohen and Gawthrop (1996, p. 78) to include the craniids (and *Phoronis*!) within an 'inarticulated' clade serving as a sister group to living rhynchonelliforms. This molecular interpretation of brachiopod evolution could endorse the monophyly of inarticulation, albeit at the expense of a polyphyletic calcitic shell.

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APPENDIX 1

Paterinate characters

The states of 39 characters used in the phylogenetic analysis of ten paterinate genera and seven other genera representing linguliform and rhynchonelliform brachiopods:

1. Convexity — biconvex (0), dorsibiconvex (1), ventribiconvex to planoconvex (2)
2. Anterior commissure — rectimarginate (0), uniplicate (1), sulcate (2)
3. Posterior commissure — dissociated (0), strophic (1)
4. Micro-ornament (larval) — smooth (0), indented with rounded pits (1), indented with hexagonal pits (2), tuberculate (3), no larval shell (4)
5. Boundary of larval shell — indistinct (0), halo (1), no larval shell (2)
6. Larval spines or tubercles — absent (0), present (1)
7. Larval shell lobate — no (0), yes (1), no larval shell (2)
8. Periostracal micro-ornamentation — none (0), pustulose (1), circular pits (2), hexagonal pits (3)
9. Periostracum — flexible (0), inflexible (1)
10. Radial ornamentation — absent (0), capillae (1), costellae (2), smooth to costellate peripherally (3)
11. Concentric ornamentation — smooth (with growth banding) (0), symmetrical fila (1), asymmetrical fila with outer faces (2)
12. Pitting of postlarval shell — absent (0), as offset depressions (1), as depressions and perforations (2)
13. Ventral pseudointerarea — pseudointerarea (0), interarea (1)
14. Pedicle opening — delthyrial (0), other (1)
15. Pedicle groove — absent (0), present (1)
16. Delthyrial cover — absent (0), pseudodeltidium (1), narrow, ridge-like (2), broad, convex (3)

17.	Shell growth of dorsal valve	hemiperipheral (0), holoperipheral or mixoperipheral (1)
18.	Dorsal pseudointerarea/interarea	absent (0), pseudointerarea (1), interarea (2)
19.	Notothyrium	absent (0), present (1)
20.	Median plate on dorsal valve	no pseudointerarea or interarea (0), no pseudointerarea or interarea median plate (1), median plate without muscle scars (2), median plate with muscle scars (3)
21.	Ventral mantle canals	baculate (0), pinnate (1), saccate (2)
22.	Ventral posterior muscle fields	sited posteriolaterally (0), sited posteriomedially (1), other (2)
23.	Inner delthyrial margins	not modified (0), strongly thickened (1), supported by short ridges (2), no delthyrium (3)
24.	Outer deltidial margins	no delthyrium (0), delthyrial cover without lateral furrows (1), pseudo-deltidium with lateral furrows (2), no delthyrial cover (3)
25.	Ventral transmedial muscle	present (0), absent (1) scars
26.	Umbonal perforation	absent (0), present, enlarged anteriorly by resorption (1), small, apical (2)
27.	Colleplax	absent (0), present (1)
28.	Pedicle nerve impression	absent (0), present (1)
29.	Dorsal anteriolateral muscle scars	present (0), absent (1)
30.	Dorsal mantle canals	baculate (0), pinnate (1), saccate (2)
31.	*Vascula terminalia*	bifurcating peripherally and medially (0), bifurcating peripherally (1)
32.	Dorsal adductor muscle scars	grouped, radially arranged (0), dispersed (1)
33.	Medial ridge	absent (0), short, posteriorly placed (1), short, in anterior part of visceral area (2), bisecting entire visceral area (3)
34.	Submedial ridges	absent (0), present (1)
35.	Shell composition	organophosphatic (0), calcitic (1)
36.	Inclination of ventral interarea (pseudointerarea)	apsacline (0), orthocline (1), procline to catacline (2), no interarea (pseudointerarea) (3)
37.	Imprinted stratiform lamination	no lamination (0), no imprints (1), with imprints (2)
38.	Free spondylium	absent (0), present (1)
39.	Paired teeth at delthyrial margin	absent (0), present (1)

APPENDIX 2

Matrix of the 39 characters enumerated in Appendix 1 and 17 genera, ten paterinate and seven representing penecontemporaneous Cambrian lingulate and rhynchonelliform brachiopods.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
Chile	2	0	1	4	2	2	2	0	1	2	0	0	1	0	0	1	0	0	0	0	3	0	0	1	1	1	1	0	1	?	1	0	0	0	1	1	0	0	0
Eoobolus	1	0	0	1	1	0	0	1	0	0	0	0	0	1	1	0	1	1	0	2	0	0	3	0	0	0	0	1	0	0	0	0	3	1	0	4	1	0	0
Botsfordia	2	0	0	1	1	1	0	1	0	0	0	0	0	1	1	0	1	1	0	2	0	0	3	0	0	0	0	1	0	0	0	0	3	1	0	4	1	0	0
Obolus	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	2	0	0	3	0	0	0	0	1	0	0	0	0	2	0	0	4	1	0	0
Fossuliella	1	0	0	1	0	0	0	2	0	0	0	0	0	1	1	0	1	1	0	2	0	0	3	0	0	0	0	1	0	0	0	0	2	0	0	4	1	0	0
Paterinia	2	0	1	3	1	0	1	0	0	0	1	0	1	0	0	0	1	2	1	3	?	1	2	3	1	0	0	0	1	1	1	1	0	2	0	0	1	0	0
Micromitra	2	0	1	3	1	0	1	0	0	1	2	0	1	0	0	3	1	2	1	3	2	1	1	2	1	0	0	0	1	2	1	1	1	2	0	0	1	0	0
Askepasma	2	0	1	2	1	0	0	3	0	0	1	0	1	0	0	0	1	2	1	1	1	?	0	0	1	0	0	0	1	?	1	1	1	3	0	0	2	0	0
Cryptotreta	0	1	1	?	1	0	0	?	0	0	1	0	1	0	0	0	1	2	1	1	1	?	0	3	1	0	0	0	1	1	1	?	0	0	0	1	2	0	0
Aldanotreta	2	2	1	2	1	0	0	3	0	0	1	0	1	0	0	2	0	0	0	0	?	?	0	1	1	0	0	0	1	?	?	?	0	0	0	0	2	0	0
Salanygolina	2	0	1	?	?	0	0	?	?	0	1	0	1	0	0	2	0	0	0	0	?	?	0	1	1	1	0	0	1	?	?	?	0	0	0	0	?	0	0
Dictyonina	2	0	1	3	1	0	1	0	0	0	2	1	1	0	0	3	1	2	1	3	2	1	1	1	1	0	0	0	1	2	1	1	0	2	0	3	1	0	0
Dictyonites	2	0	1	0	1	0	1	0	0	0	2	2	1	0	0	3	1	2	1	3	?	1	1	1	1	0	0	0	1	?	?	?	0	0	0	2	1	0	0
Lacunites	2	0	1	0	1	0	1	0	0	0	2	1	1	0	0	3	1	2	1	?	?	1	1	1	1	0	0	0	1	?	?	?	0	?	0	2	1	0	0
Kolihium	2	0	1	?	1	0	1	0	0	0	2	1	1	0	0	3	1	2	1	?	?	?	0	1	1	0	0	0	1	?	?	?	0	?	0	2	1	0	0
Glyptoria	1	1	1	4	2	2	2	0	1	1	0	0	1	0	0	0	1	2	1	1	1	2	0	3	1	0	0	0	1	1	1	1	1	0	1	0	0	1	1
Kutorgina	2	0	1	4	2	2	2	0	1	0	0	0	1	0	0	1	1	2	1	1	?	2	0	2	1	2	0	0	1	?	?	1	0	0	1	0	0	0	0